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PROFESSOR THOMAS H. BRYCE, UNIVERSITY OF GLASGOW
PROFESSOR EDWARD FAWCETT, UNIVERSITY OF BRISTOL
PROFESSOR J. P. HILL, UNIVERSITY OF LONDON
PROFESSOR G. ELLIOT SMITH, UNIVERSITY OF MANCHESTER
PROFESSOR ARTHUR KEITH, ROYAL COLLEGE OF SURGEONS, LINCOLN'S-INN-FIELDS, LONDON, W.C.

(*All Communications relating to the Journal should be addressed to the* ACTING EDITOR, *Professor Keith.*)

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JOURNAL OF ANATOMY

THE EVOLUTION OF THE TETRAPOD SHOULDER GIRDLE AND FORE-LIMB.

By Lieut. D. M. S. WATSON, M.Sc., R.N.V.R., *Lecturer in Vertebrate Palæontology in University College, London.*

FROM the beginning of the study of osteology the Tetrapod shoulder girdle has been discussed by innumerable anatomists. Left by Cuvier and Owen in a state of perfect simplicity so far as concerned its morphology and nomenclature, it has gradually become more and more confused through the investigation of its development and the discovery of new fossil material.

This confusion is partly genuine, depending on actual and real differences of opinion about the homologies of its elements, and partly depends on misuse of names. I have had evidence that a thorough study of the literature of this region by one who is not personally acquainted with actual material leads inevitably to the acceptance of views which cannot be made to agree with any reasonable and consistent scheme of its evolution.

In my opinion morphological questions must be approached from below—that is, from the standpoint of the truly primitive members of the phylum—and the changes in relation of the individual regions of the organs considered traced upwards from this beginning. The series so constructed must then be checked by a study of the development in such forms as can be obtained, and finally, if it be possible, a functional explanation must be found for the observed series of changes.

It is my purpose in this paper to study the mode of origin of the mammalian shoulder girdle in this way, because material for this study is more abundant and more readily treated than that for other groups, and because, as the nomenclature of the mammalian shoulder girdle is the standard to which others must be reduced, such a study is an essential preliminary to their investigation.

I have in a previous paper endeavoured to show that the embolomerous amphibia are the most primitive as they are the oldest known Tetrapods, and that from them the Cotylosauria and the rachitomous amphibia are alike derived.

The well-known Embolomeri are primitively aquatic animals, whilst

the best-known Rachitomi (Eryops, *e.g.*) and all the early Cotylosaurs are essentially land animals, the advances in their structure being almost all such as fit them for a thoroughly terrestrial life.

As I shall treat of the shoulder girdle of Embolomeri in another connection, this paper will begin with the rachitomous amphibia and pass on through the Cotylosauria and various types of Anomodonts to the mammalia, along a series which is now recognised by the majority of palæontologists as a true although approximate phylogenetic series.

For convenience the paper is divided into two parts, the first dealing with facts and interpretations only so far as they concern individual forms, the restoration of the musculature and the possible motions being the more important items under the latter head. The second part deals with changes and their functional meanings.

Rachitomous Amphibia.

The shoulder girdle is now known in many forms of land-living rachitomous amphibia. Eryops, Cacops, Trematops are well-known Artinskian (Lower Permian) forms agreeing in main features. Eryops as the largest type may be briefly described here; the whole structure has been figured by Cope and Case (*Carnegie Inst. of Washington Pub.* 146, 1911, pp. 99–100, pls.) and Moodie. The "primary" shoulder girdle consists of a single large element on each side. This bone has a large scapular blade lying over the ribs of the anterior part of the round body of the animal. From the outer surface of the bone rises a powerful process whose posterior surface forms the anterior end of the glenoid cavity. The articular surface of this cavity forms a strip, shallow dorso-ventrally, but of considerable length; its anterior end faces backwards. In the middle of its length it lies at its most dorsal position and faces directly outwards. Finally, posteriorly it faces outwards and forwards and somewhat dorsally. The coracoidal end of the bone lies ventral to the glenoid cavity, and forms a small thin plate which is somewhat turned in towards the mid-ventral line.

The scapula-coracoid is pierced by three foramina, first accurately described by Williston. These are the *supraglenoid*, passing through from the back of the scapula above the glenoid cavity to the inner surface, where it opens into a pit; the *glenoid*, opening from the outer surface just below the anterior part of the glenoid cavity and passing through the bone to open into the same pit as the supraglenoid; and the *precoracoid* foramen, opening through the precoracoidal region of the bone. The precoracoid foramen transmitted the supracoracoid nerve; what passed through the other openings is quite uncertain, but they perhaps received extensions of the synovial cavity surrounding the head of the humerus.

The interclavicle is a small oval plate of bone lying in the mid-ventral line in the region of the anterior margin of the coracoidal end of the "scapulo-coracoid."

The central region of the ventral surface of the interclavicle bears a somewhat faint ornament of pits, similar to that of the dorsal surface of the head, and showing beyond all question that the interclavicle is a dermal bone lying in the skin and having no muscle insertions on its ventral surface. The clavicle is a slender bone, bent so as to form about a quadrant of a circle, with an unornamented upper end of nearly circular section, but bearing a groove on its posterior surface which receives the lower end of the cleithrum. The lower end of the clavicle is flattened and expanded antero-posteriorly so that it forms a relatively broad plate of bone which overlies the recessed antero-lateral part of the ventral surface of the interclavicle, and like that bone has its outer face covered with a pitted ornament.

The cleithrum is a very large bone forming a cap over the dorsal end of the scapula, and provided with a long slender process applied to the front edge of that bone and itself covered below by the upper end of the clavicle.

The humerus is a short, very massive bone with an exceedingly short shaft and much-expanded ends, whose broad surfaces make a considerable angle (about 90°) with each other.

The head of the humerus in old, well-ossified individuals shows a sharply marked articular area in the form of a long strip winding round the cylindrical proximal end like the thread of a screw. The only other features of the humerus to which it seems necessary to call attention here are the large, well-developed entepicondyle, the presence of a special very strong process arising from the shaft above and behind the ectepicondyle, and the general excellence of the ossification in old individuals.

The peculiar shape of the glenoid cavity and of the articular strip wound round the head of the humerus shows that the humerus has its motions very strictly limited; it is incapable of any rotation on its long axis, and that axis must be so placed that it lies nearly parallel to the ground, but even at its position of extreme depression the distal end is higher than the glenoid part. Finally, its only possible motion is such that a point on the distal extremity when viewed directly laterally moves along a small segment of a large circle placed parallel to the animal's sagittal plane, with the chord of the segment placed nearly horizontally; in other words, as the humerus moves forwards its outer end is first slightly depressed and then raised again.

This type of motion, in which the humerus is restricted to one definite

track both in its forward and backward motion, is common to very many early Tetrapods, and its significance and the musculature which goes with it will be considered in this paper under the head of Pelycosauria.

The enormous size of the upper part of the cleithrum in the majority of Rachitomi shows that that region was of functional importance, and it seems probable that it gave origin to the scapular part of the deltoid, which muscle may in these animals have formed a continuous sheet having its origin from the outer surface of the cleithrum and the posterior and lateral margins of the clavicle and interclavicle.

The rachitomous amphibian Archegosaurus is known by a very large number of specimens, which allow us to trace the origin and progress of ossification in the shoulder girdle.

In fully-grown old individuals, which are not at all common, the scapulo-coracoid greatly resembles that of Eryops, having a large scapular blade and a smaller coracoidal part lying below the glenoid cavity. The articular surface is a screw-shaped strap like that of Eryops, except that it is abruptly truncated posteriorly, in the specimens I have seen, obviously owing to the persistence of a small cartilaginous region.

The cleithrum is quite similar to that of Eryops, and the clavicle and interclavicle only differ in the widening of their ventral surface, which is apparently an aquatic adaptation.

The evidence of young specimens shows conclusively that the scapulo-coracoid is really a single bone, ossification beginning in the scapula blade just above the glenoid cavity at the hinder margin, spreading gradually through the scapular part, and only invading the coracoidal region in individuals which are about three-quarters of the largest size.

The evidence given by the less abundant material of Actinodon, which has recently been described by Thévenin (*Ann. de Palæontologie*, 1910), supports the conclusion that the scapulo-coracoid of certain rachitomous amphibia may be only a single bone, the ossification of which begins in the scapula. In this connection it may be recalled that no one has demonstrated the presence of sutures in the scapulo-coracoid of any Lower Permian amphibian.

Cotylosauria.

So far as its skull is concerned, the Lower Permian Cotylosaur *Seymouria* is the most primitive of known reptiles.

The limbs of this animal, both fore and hind, are also so similar to those of Eryops and its allies that when their bones were first discovered isolated they were described as an amphibian, Desmospondylus, and their

true position was only realised by Professor Williston when he obtained a complete skeleton.

Considering this extraordinary primitiveness in nearly all regions of the skeleton, it is remarkable that the shoulder girdle is in some ways specialised.

The scapulo-coracoid resembles that of Eryops in its general characters, and has the same type of screw-shaped glenoid cavity. The extreme posterior end of this cavity was, however, unossified, being cut by a cartilage face in the only described specimen. There is a definite suture between the scapular and coracoid regions, running so as to divide the anterior region of the articular surface of the glenoid cavity horizontally.

There is no cleithrum. The clavicle and interclavicle on the whole resemble those of Eryops, but the latter bone has a larger area, with a short posterior stem and produced lateral angles. The clavicles extend up to the top of the scapula, no doubt secondarily following the loss of cleithra.

The *Diadectids* are a group of Cotylosaurs which, though more advanced than Seymouria, are still in many ways very primitive reptiles.

The scapulo-coracoid is a bone extremely similar to that of Eryops, agreeing with it in all important features, including the form and position of the glenoid cavity. No specimen has been described as showing any sutures separating the scapular from the coracoidal ends.

The interclavicle is a long straight flattened bone whose anterior end is surrounded by the inner ends of the clavicles, which have firm sutures with it.

The clavicle is a massive bone bent round to fit the body, and slightly expanded ventrally where it articulates with the interclavicle and its fellow. Neither clavicle nor interclavicle is in any way ornamented, and all their surfaces may have served as muscle attachments.

The cleithrum is a slender bone partially capping the scapula.

The Diadectid humerus is very short and massive, differing from that of Eryops only in the presence of a foramen piercing the very large entepicondyle, and in the slightly more proximal position of the tuber for the deltoid insertion.

The powerful process in the ectepicondylar region which probably gave origin to the supinator longus or brachialis anticus is identical in the two forms.

The *Captorhinidæ* are an important group of Cotylosaurs closely related to the ancestry of the Anomodontia, and hence of the mammals. No well-preserved shoulder girdles have been described, and none is available to me. In the large form Labidosaurus, there are three elements in

each side of the cartilaginoid shoulder girdle, the glenoid cavity being screw-shaped and much resembling that of the Pelycosaurs.

The humerus has expanded ends and is twisted, but differs from those of Eryops, Seymouria, and Diadectes in being much more lightly constructed and lacking the powerful process for the brachialis anticus. Judging from the well-ossified head of the humerus of Captorhinus, the glenoid cavity in that form is not typically screw-shaped, but in the absence of well-preserved shoulder girdles it is unnecessary to discuss its possible motions.

The Pariasauridæ, a family of Cotylosaurians, includes a series of large animals of very heavy build whose generic separations are still largely undefined. In the shoulder girdle and humerus they present such marked differences that no general statements are possible, and it is necessary to describe individual types in some detail:—

Embrithosaurus sp.?, the individual of which the skull was described by Watson, *Proc. Zool. Soc.*, 1914, pp. 155–180, figs. 1, 2, 4, 5, from the Tapinocephalus zone, Middle Permian, of Hottentot's River, Dist. Beaufort West, Cape Province (fig. 1).

The scapulo-coracoid of this form has a short narrow scapula blade with whose anterior margin a small cleithrum is fused. At the level of the lower end of this bone the front margin of the scapula is thickened and everted, forming a distinct acromium, which terminates below in a margin which passes inwards to the front face of the scapular blade so as to leave a distinct rounded notch, the first representative of the mammalian supraspinus fossa. Posteriorly the scapula is thickened, and with the posterior upper corner of the precoracoid, which is not visibly delimited by suture, forms a powerful outstanding process which carries the anterior end of the glenoid cavity.

The glenoid cavity is screw-shaped, but differs from that of Diadectes, etc., in having a much deeper articular surface in proportion to its length; its anterior part faces downwards, backwards, and slightly outwards; the posterior part faces directly outwards. The lower margin of the glenoid cavity is notched, the notch forming the upper border of a small pocket from the bottom of which the precoracoid foramen starts and passes through the bone. Below the humeral articulation the precoracoid and coracoid form a large flat area.

The clavicle is a massive bone articulating with the front surface of the acromium and forming a quadrant of a circle, so that its lower end is applied to the front face of the interclavicle and just touches its fellow of the opposite side.

The interclavicle is T-shaped, its flat front surface giving attachment

to the clavicle. The stem is long, narrow, but slightly swollen posteriorly, and of considerable thickness.

The humerus of this individual was not preserved.

The type specimen of *Bradysaurus baini* (Seeley), from the Tapinocephalus zone, Middle Permian, has been well described by Seeley, *Phil. Trans.*, B, vol. 183, pp. 311–370, pls. 17–23.

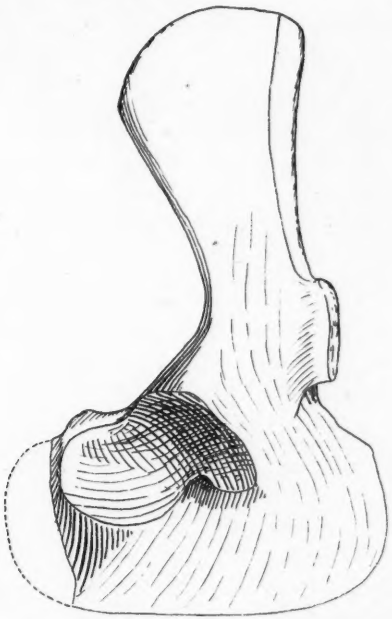

FIG. 1.—Right scapulo-coracoid and cleithrum of *Embrithosaurus* sp., external surface. $\times \frac{1}{12}$.

The clavicle and interclavicle are indistinguishable from those of the specimen described above, but the scapulo-coracoid is very different.

The scapula blade is much narrower, the acromium less everted and more markedly distinct from the rest of the bone. The glenoid cavity is still screw-shaped, but its articular area is much deeper in proportion to its length, and its anterior end looks much more directly downwards—in fact, it scarcely faces at all backwards.

Finally, the whole lower end of the bone is much shorter from front to back, the precoracoidal region in particular being much reduced.

The humerus of a species of this genus is very well preserved in

a skeleton I collected on Hottentot's River, which shows that, as Professor Seeley suspected and Dr Broom has already shown, the two ends, instead of being nearly parallel as in the British Museum specimen, really make a considerable angle (about 50°) with one another (fig. 2).

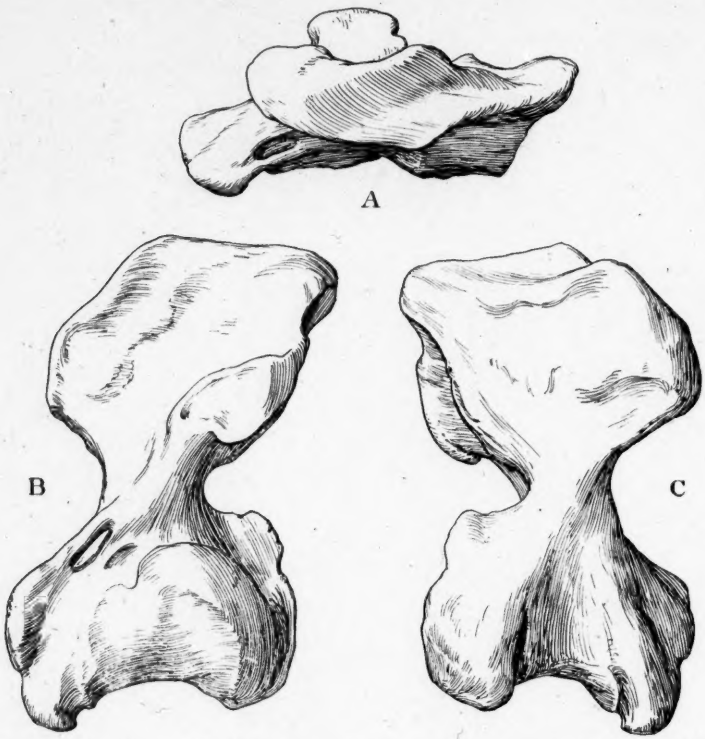

FIG. 2.—Left humerus of *Bradysaurus* sp. Dorsal, ventral, and proximal views, to show especially the screw-shaped surface for articulation with the glenoid cavity. × ½.

When correctly articulated, the humerus stands out at right angles to the animal's body, with the broad plane of the upper end inclined downwards in front and the broad plane of the distal end nearly parallel to the ground, as it is placed on Professor Seeley's figure.

The lower end of this, as of all other Pariasaurian humeri, is remarkable for the very small relative size of the entepicondyle when the bone is compared with that of any other Cotylosaur. The radius and ulna,

which are well preserved in both the skeletons available, fit their articulations on the humerus with great accuracy, and completely justify the position given them by Seeley. In the normal position they stand at right angles to the expanded lower end of the humerus, and are placed nearly perpendicular to the ground, separated from their fellows of the other side by the length of the two humeri plus the distance between the two glenoid cavities.

The vertical position of the fore-arm, by enabling the main stress in its components to be a compression on the radius and the tension in the flexor muscles of its palmar surface to be very small, is the explanation of the very small entepicondyle of the humerus of the animal.

The deep sigmoid notch and pronounced olecranon strictly limit the possibility of motion of the fore-arm to a small flexion and extension in the plane containing these bones and the main axis of the humerus.

Embrithosaurus and Bradysaurus are of Tapinocephalus zone age—that is, Middle Permian. In the Upper Permian Cistecephalus zone of South Africa and of the Dwina region of Russia we meet other Pariasaurs. Of these, the commonest South African type is Propappus, whose shoulder girdle as described by Broom resembles that of Bradysaurus in all ways, including the shape of the glenoid cavity.

The scapulo-coracoid of one of Professor Amalitzki's Russian Pariasaurs is represented in the British Museum by a cast from which fig. 3 is drawn. It closely resembles that of Bradysaurus in many ways, but differs in the higher position of the acromium, and especially in the complete loss of the screw-shaped glenoid cavity, the articular surface being now represented by a shallow pit whose posterior margin lies at the extreme posterior edge of the bone.

The shoulder girdle of Pariasuchus, from the Cistecephalus zone of the Niewveld, as it has been described by Broom and Haughton (*Ann. So. Afr. Mus.*, vol. xii. p. 22, pl. iii.) is of very great interest.

The scapula blade resembles that of any other Pariasaurian in having a pronounced outstanding acromium, and the general shape of the pre-coracoid and coracoid region is also Pariasaurian, but the glenoid cavity is quite unlike that of any other member of the group. Instead of facing outwards and being formed by a depression of the outer surface of the shoulder girdle, it faces backwards and notches the posterior surface so that its position is shown from the visceral surface. This new position and shape of the glenoid cavity means that the mode of moving the fore-limb differed very considerably in Pariasuchus from that in all other known members of the group, and explains the remarkably individual form of the humerus, which has the antero-external corner of the head to which

the m. supracoracoideus and m. scapulo-humeralis anterior were attached much produced.

The position of the mounted skeleton photographed by Broom and Haughton (*op. cit.*, pl. v.) is, I believe, nearly correct, and is one into which it is quite impossible to place Bradysaurus or Embrithosaurus without, as in the Cape Town specimen of the latter genus, dislocating all its joints.

FIG. 3.—Left scapulo-coracoid of *Pariasaurus Karpinskyi*, Amalitz., external surface. $\times \frac{1}{3}$.

The Pariasaur bones at my disposal do not show the muscle insertions sufficiently plainly to allow me to endeavour to reconstruct the musculature.

PELYCOSAURIA.

The group Pelycosauria includes a large number of considerably diverse forms, some of considerable size, others comparatively small. The shoulder girdle and fore-limb consequently present considerable variations throughout the group, but the fundamental plan is identical in all.

Dimetrodon, a large advanced form, is on the whole the best known, and is described here as a standard.

The scapulo-coracoid is a large bone with a large flat scapula blade lying parallel to the ribs; its anterior edge is thin, whilst the hinder part is much thickened and rounded. The lower margin of the scapula is divided into two parts, the anterior having a long and close suture with the precoracoid, the posterior a more open suture with the coracoid. At the posterior end of the suture between the scapula and precoracoid the two bones are much thickened, forming a stout process bounded below by a deep fossa from

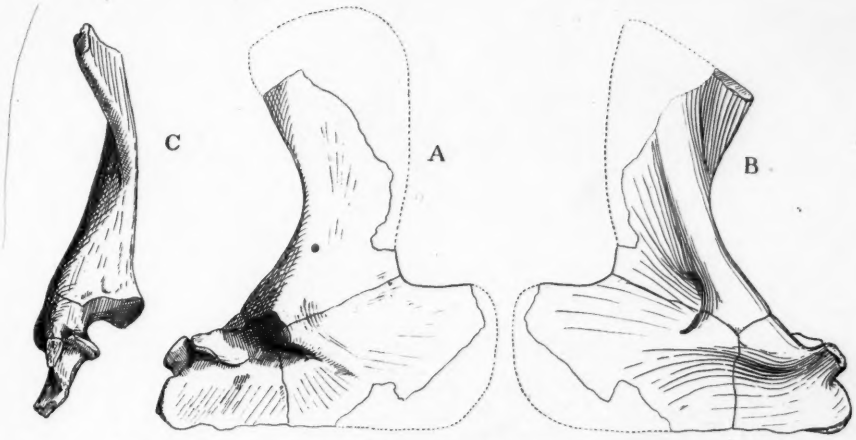

FIG. 4.—Right scapula, precoracoid, and coracoid of *Dimetrodon* sp. External (A), internal (B), and posterior (C) views. $\times \frac{1}{5}$.

which the precoracoid foramen starts. The posterior face of this process forms the anterior part of the glenoid cavity, facing backwards, slightly downwards, and scarcely at all outwards. The glenoid cavity has a narrow screw-shaped articulating face resembling that of Eryops, the posterior half of which lies entirely on the coracoid; this region faces upwards and outwards.

This glenoid cavity differs from that of Eryops in that the articular surface is wider in proportion to its length and that the anterior part lies higher than the posterior.

Below the level of the glenoid cavity the coracoid and precoracoid are continued down towards the middle line, forming a large flat area. On the posterior edge of the coracoid is a powerful inwardly and backwardly directed process, presumably for the insertion of the coraco-brachialis longus.

On the visceral surface the scapulo-coracoid shows a large generally smoothly-lying surface bounded behind by the thickening of the posterior margin of the scapula and coracoid. From this a subsidiary ridge runs forwards on the precoracoid so as to form a deep fossa, lying over the suture between the precoracoid and scapula, into which the foramina supra-genoideus and precoracoideus open. On the lower side of the ridge on the precoracoid is a very pronounced depression partly on the precoracoid and partly on the coracoid, which appears to have housed a large subcoracoid muscle. The inner surface of the posterior upper part of the scapular blade is depressed and separated by a low ridge from the rest of the surface; it passes by a distinct wide depression to the posterior margin of the scapula, and probably denotes the position of the belly of a large sub-scapularis muscle.

Membrane Bones.

The interclavicle is a long straight flattened bone lying on the ventral surface of the animal and extending far behind the coracoids.

At its anterior end the interclavicle is widened into a lozenge-shaped head, whose lower face is largely covered by the clavicle.

The clavicle is a bone which articulates with the front edge of the scapula as a narrow bar which widens as it is followed downwards until it expands into a broad flat plate underlying the interclavicle. A cleithrum does not occur in Dimetrodon, but a small splint representing this bone occurs in the nearly allied *Clepsydrops natalis* and in Edaphosaurus.

Humerus.

The humerus of Dimetrodon is a stout bone with much-expanded upper and lower ends placed nearly at right angles. The proximal end of the bone is crossed obliquely by a narrow articular strip which begins on the dorsal surface above the deltoid crest and finishes ventrally at the posterior margin of the expanded head. From the anterior edge of the lower face of the expanded upper end a powerful plate-like delto-pectoral crest projects downwards. From this crest a low ridge crosses the shaft and becomes continuous with the posterior margin of the enormous entepicondyle. This region is pierced by a large foramen lying high up towards the shaft. Placed right at the distal end of the bone in the direct line of the shaft, and lying almost entirely on the anterior and lower surface of the expanded end, is a very distinct hemispherical articular surface for the head of the radius.

If the radial condyle be placed facing upwards, the equally distinct face for the ulna lies in the main internal but partly below it; it forms a some-

what spheroidal face mainly on the end, but also to a slight extent on both broad surfaces, of the humerus.

The ectepicondyle is massive and directed somewhat backwards; proximal to it and lying in front so that the two enclose a distinct channel is a small but powerful process for the brachialis anticus.

Fore-arm.

The radius is a straight rod with a hemispherical cup for the condyle on the humerus. The ulna is chiefly remarkable for the possession of a very large olecranon and of a deep sigmoid notch.

Freedom of Motion of the Fore-limb.

The narrow screw-shaped articular surfaces of the glenoid cavity and the head of the humerus fit extremely accurately in old individuals, and fix the position and possible motions of the humerus with great exactness.

When the humerus projects at right angles to the body, its principal axis in Dimetrodon lies nearly parallel to the ground. The bone is incapable of any rotation about its axis whilst it retains a fixed position, and can only move so that a point on the distal end describes a segment of a circle whose chord is higher anteriorly than posteriorly. When the humerus is carried backwards the anterior margin is depressed relatively to the posterior. The humerus can scarcely be placed much in advance of a right angle to the animal's principal plane, and its range in motion is extremely limited; it can perhaps turn through about 50°.

The fore-arm has considerable freedom of motion on the humerus. At its normal position it stands at right angles to the expanded lower end of the humerus, and makes an angle of about 30° with the ground. It can be moved in and out through a somewhat small angle restricted by the deep sigmoid notch of the ulna, whilst the spheroidal shape of the ulnar articulation on the humerus allows of some movement in a plane at right angles to the long axis of the humerus.

The walk of Dimetrodon must have taken place somewhat in the following manner:—

When the animal is standing with the left fore-leg in the normal position, the right humerus is advanced, raising its outer end and its anterior edge; the fore-arm, lying nearly parallel to the ground, is extended as much as possible and the palm placed on the ground. The humerus is then retired and the elbow flexed. The combined motions raise the glenoid cavity, owing partly to the depression of the outer end of the humerus and partly to the depression of its anterior edge; they also swing the body

across so that the hand gets nearer the middle line. Finally, the fore-arm is pulled backwards on the humerus, still further raising and driving forward the animal. At or before this stage the left arm is advanced and repeats the same process. The whole anterior part of the body is thus swung from side to side at each stride. The width of the track is very considerable, being equal to the width between the distal ends of the two humeri, and the stride is very small. Measurements suggest that a rather small Dimetrodon might make a track 16 inches wide, with a stride of perhaps 6 inches to 8 inches.

The bones of Dimetrodon at my disposal show certain muscle insertions clearly, but none shows all of them. I collected from the Craddock bone bed, however, the upper end and part of the distal half of a small primitive Pelycosaur humerus (? Varanosaurus) which shows all the muscle insertions diagrammatically. These agree closely with such as are known in Dimetrodon, and there can be no doubt that the musculature and mechanics of the two animals are quite similar.

The positions of the insertions of the muscles on this humerus will be best understood from the figures; their determination rests on a comparison with Sphenodon, whose musculature must be very similar to that of the Pelycosaurs (fig. 5).

The important features are the large size of the insertions of the deltoid, pectoral, and supracoracoid muscles; the somewhat distal position of the powerful insertion which seems to be for the latissimus dorsi and scapulo-humeralis posterior; and the well-marked confluent insertion of the sub-scapularis and subcoracoideus. The coraco-brachialis brevis is short but wide, the coraco-brachialis longus much more considerable.

The muscle insertions on the lower end of the humerus cannot be safely distinguished. There are powerful flexor insertions on the huge entepi-condyle, and the dorsal surface of the ectepicondyle has a very powerful insertion for an anconeus quartus.

Like other Tetrapods, Dimetrodon is supported by its limbs, which are compound levers held in place by muscles which act as tensile members.

The stress developed in the muscles of the fore-limb of Dimetrodon may be grouped as follows:—

1. The palm resting on the ground, contraction of the flexor muscles attached to the entepicondyle and to the carpal region raises the humerus if that bone does not revolve on its axis. The anconeus quartus, passing from the ectepicondyle to the upper end of the olecranon process of the ulna, assists this motion.
2. The elbow is flexed by the biceps and brachialis internus.
3. The elbow is extended by the triceps.

The fore-arm is thus held or moved in definite directions in relation to the humerus by the action of two opposed pairs of muscles, the flexors and extensors and the biceps and triceps.

The fact that, whilst the weight is applied at the upper end of the radius and ulna, these bones are only inclined at a very small angle to

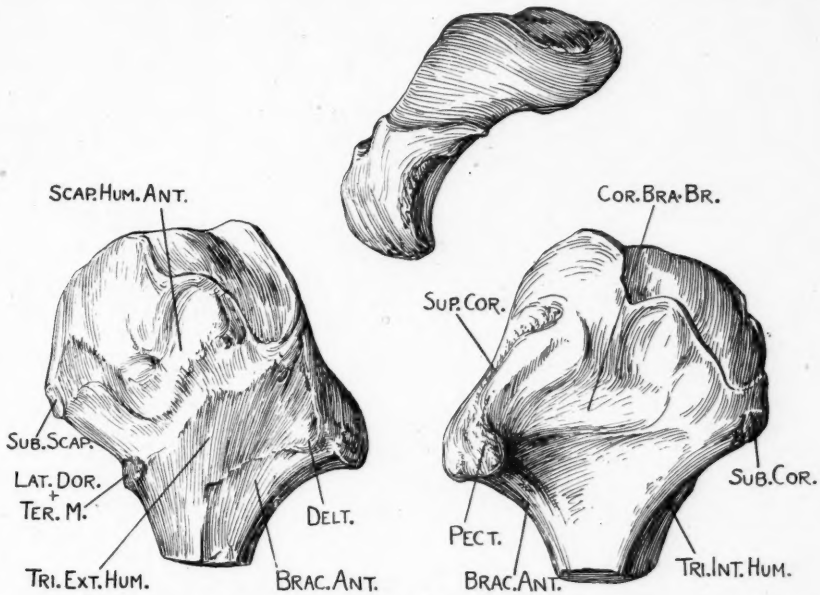

FIG. 5.—Dorsal (A), ventral (B), and proximal (C) views of the upper end of a small Pelycosaur humerus, Varanosaurus? ×2.

Brac. Ant., origin of brachialis internus; Cor. Bra. Br., insertion of coraco-brachialis brevis; Delt., insertion of deltoid; Lat. Dor. + Ter. M., insertion of latissimus dorsi and scapulo-humeralis posterior; Pect., insertion of pectoralis; Scap. Hum. Ant., insertion of scapulo-humeralis anterior; Sub. Cor., insertion of subcaracoideus; Sub. Scap., insertion of subscapularis; Sup. Cor., insertion of supra-coracoideus; Tri. Ext. Hum., origin of external humeral head of triceps; Tri. Int. Hum., origin of internal humeral head of triceps.

the ground, throws a very heavy strain on the flexor muscles. This strain is lessened by removing their insertion on the humerus as far as possible from the hinge of the fore-arm with that bone, so that, as the angle at which the muscles are inserted on the fore-arm is increased, the vertical component of their pull becomes greater. This is the explanation of the very large entepicondyle of the early Tetrapod humerus.

The flexors of the fore-arm and the anconeus quartus produce a couple which tends to rotate the humerus on its axis so that the anterior margin

moves upwards. The stresses developed by the other muscles passing from the humerus to the fore-arm will very nearly balance one another.

The humerus may now be regarded as a lever jointed to the shoulder, supported at its distal end, and in addition acted on by a couple tending to rotate it.

From the character of its glenoid articulation, it cannot be depressed or rotated. So far as concerns depression and elevation, it is held in place by the powerful pectoral and coraco-brachial muscles, arising respectively from the outer margins of the interclavicle and the ventral surface of the belly, and from the extensive area of coracoid and precoracoid lying below the glenoid cavity. These muscles are opposed by the subscapularis, latissimus dorsi, scapulo-humeralis posterior, and deltoid muscles, arising from the upper posterior corner of the inner surface of the scapula, the dorsal body wall, the upper part of the outer face of the scapula, and the cleithrum (if present) and clavicle respectively.

The tendency to rotate the humerus on its axis is opposed by the subscapularis, scapulo-humeralis posterior, and latissimus dorsi, and the pectoral, which together form a couple of the opposite sign. This couple is itself opposed by another, formed by the subcoracoideus and the deltoid.

The large powerful pectoral crest of Dimetrodon is an adaptation to increase the moment of pull of the pectoral muscle, which in any case acts at a considerable mechanical disadvantage. The advance of the humerus is brought about mainly by the action of the supracoracoid muscle and perhaps the scapulo-humeralis anterior. The lower clavicular portion of the deltoid also draws the humerus forward. The humerus is retired by the action of the subcoracoideus, the coraco-brachialis longus, and the posterior part of the pectoral.

The other Pelycosaurs agree in the general principles of their fore-limbs with Dimetrodon, but present the following important variants:—

1. Varanoops, one of the most primitive members of the group, is devoid of an ossified coracoid, the glenoid cavity being abruptly truncated by a cartilaginous face behind the precoracoid and scapula. The anterior end of the glenoid cavity, which has the usual screw shape, lies very low down in the animal, as it does also in its near ally Varanosaurus, where, however, the coracoid is ossified and the precoracoid only takes a small part in the formation of the glenoid cavity.

2. The Ophiacodontidæ are large reptiles in many ways intermediate in structure between the Poliosauridæ, of which Varanoops is a member, and the group containing Dimetrodon. In Ophiacodon itself the glenoid cavity is screw-shaped like that of Dimetrodon, but its anterior part

lies somewhat more ventral to the posterior part than in the more advanced genus.

The undetermined Ophiacodont scapulo-coracoid from the Craddock bone bed figured by Williston (p. 50, fig. 26B) generally resembles that of Ophiacodon, but is of importance because it shows that in these animals the precoracoid plays only a small part in the glenoid cavity.

Deinocephalia.

Apart from those of the Pelycosaurs, the oldest and most primitive shoulder girdle of a mammal-like reptile which is known is that which, found in the copper-bearing sandstones of Middle Permian age in the department of Orenburg and the Urals, was referred by Seeley, with great probability of correctness, to the Deinocephalian Rhophalodon. (Only two types of scapulo-coracoids have been described from the Orenburg beds, one being certainly Labyrinthodont. Only Labyrinthodonts, Deinocephalia, and a single very small Cotylosaur are known from other bones.)

The shoulder girdle of "Rhophalodon" is represented in the British Museum by casts of the glenoid region of the right side and the scapula broken off through the top of the glenoid cavity of the left side. These fragments are of identical size, and appear to have belonged to the same individual; they were figured by H. v. Meyer (*Palæontographica*, Bd. xv. pl. xvii. figs. 1–2, pl. xviii. figs. 1–2) as Eurosaurus, a Labyrinthodont. From these casts my figures have been drawn, the outline depending on a badly preserved specimen figured by Eichwald and Seeley.

The scapula has a large considerably curved blade with a thin anterior border and a massive thickening along its posterior edge. The ventral end of the scapula has a long straight suture with the precoracoid, and a much shorter connection with the coracoid.

The glenoid cavity is definitely screw-shaped, but its articular surface is relatively wide, and its anterior end, which is carried almost entirely by the scapula and only to a very small extent by the precoracoid, faces downwards, outwards, and scarcely at all backwards. The posterior part of the glenoid cavity faces upwards, and is entirely supported by the coracoid. The outer surface of the precoracoid is raised into a very definite ridge running forward from the upper anterior corner of the glenoid cavity. Ventral to the ridge the bone is depressed, forming an open pocket from which the precoracoid foramen starts.

On the visceral surface the thickened posterior margin of the scapula forms a distinct ridge, which is sharply marked off below by the deep pocket into which the precoracoid foramen opens. The precoracoid is crossed by

a low ridge, the surface of the lower part of the bone and of the coracoid being depressed to form a shallow hollow.

No complete well-preserved humeri are known, but fragments differ chiefly in their small size and greater slenderness from that of Titanosuchus, a South African Deinocephalian. They indicate an elongated humerus with wide proximal and distal ends set at a considerable angle to one another. The humerus of Brithopus, which may probably be Rhophalodon, has a comparatively small entepicondyle and an ectepicondylar foramen.

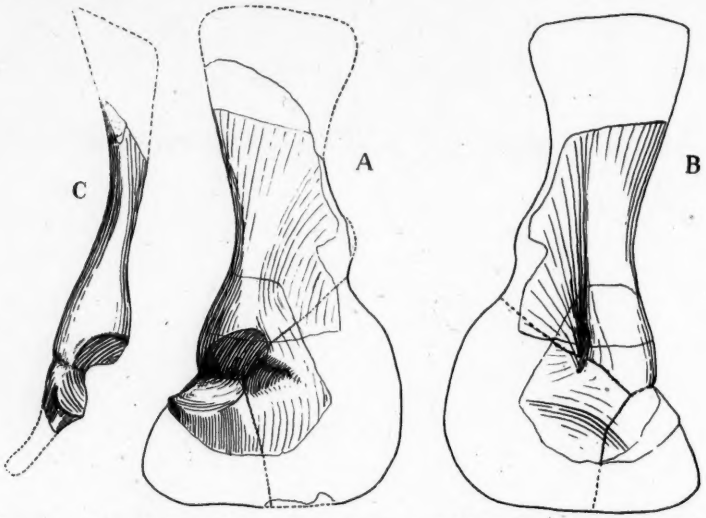

FIG. 6 —"Rhophalodon," Deinocephalian from the Middle Permian sandstones of the Dist. of Kargalinsk in the Urals. Outer (A), inner (B), and posterior (C) views of the right scapula, coracoid, and precoracoid. Shaded portions from two casts of right and left bone in the British Museum; outline from Professor Seeley. $\times \frac{1}{3}$.

The material at our disposal does not allow of a definite statement of the freedom of motion of the fore-arm in Rhophalodon, but the form of the screw-shaped glenoid cavity shows that the humerus had only a limited power of conical motion and was in the main restricted to motion in a plane lying nearly at right angles to the animal's axis and passing down at an angle of about 45° with the ground from the front to the back.

The shoulder girdle of the large South African Deinocephalia, which are of somewhat more advanced structure and probably later in date than Rhophalodon, has been described by Dr Broom (*Phil. Trans.*, Ser. B, vol. 206, pl. i. figs. 1–5) and by the present author (*Proc. Zool. Soc.*, 1914,

p. 764, fig. 11). The scapula of the huge Tapinocephaloid Phocosaurus is a flat bone with slightly thickened posterior edge; it has a long straight suture with the precoracoid, and posteriorly bears the upper part of the glenoid cavity. The precoracoid has long sutures with the scapula and coracoid, and takes no part in the formation of the glenoid cavity; its outer surface is flat, there being no ridge descending from the upper edge of the glenoid cavity; the precoracoid foramen is small. The coracoid is a relatively large bone carrying the posterior and lower part of the glenoid cavity, which faces upwards and outwards. The inner surface of the shoulder girdle is a smooth curve with a small sharply depressed pocket into which the precoracoid foramen opens.

The humerus is massive, with widely expanded upper and lower ends set at a considerable angle with one another. The head is straight when viewed from its broad plane, the articular region being cylindrical, extending round for some distance on to the dorsal surface of the bone.

The ulna has a short olecranon, but the sigmoid notch is shallow.

If, as is justified by all analogy, we place the ventral edge of the precoracoid and coracoid parallel to the middle line of the animal, then the scapulæ slope forwards so that, as in the living Monotremes, the dorsal end of the bone lies considerably in advance of its ventral portion.

The cylindrical head of the humerus and corresponding shape of the glenoid cavity suggest that there was considerable freedom of motion about an axis lying nearly horizontally but inclined down at about 30° in front—that is, that the humerus could be raised and depressed in a plane at about 60° with the ground. In a direction at right angles to this the possible motion must have been very small. Finally, there can have been little or no rotation of the humerus about its own axis. In the normal position the humerus stood nearly parallel to the ground, and with its axis directed outwards and backwards at about 60° to the animal's length.

Theriodontia, Sub-order Gorgonopsia.

Only one Gorgonopsian shoulder girdle has been described, and that shortly and incompletely by Haughton and Broom, *Ann. So. Afr. Mus.*, vol. xii. pp. 30–32, pl. vi.

In this form, *Scymnognathus tigriceps* from the Upper Permian Cistecephalus zone, the scapula is very short and broad, thickening behind and below to support the upper part of the glenoid cavity, which faces outwards, downwards, and backwards. The precoracoid is a rather small squarish bone having long sutures with the scapula and coracoid, and perforated by a small foramen near its upper posterior corner. The bone seems to be otherwise featureless. The coracoid is large, longer than the precoracoid,

and carrying the lower half of the glenoid cavity, which faces outwards and upwards. Behind the glenoid region the coracoid is produced backwards in a long, powerful process. This scapulo-coracoid generally resembles that of a Tapinocephaloid, but differs in the more anterior position of the lower part of the glenoid cavity, which also is much more nearly vertical in position, facing more outwards and less upwards than in the more primitive group.

Fig. 7.—Right scapula, with fragments of the precoracoid and coracoid attached, of Inostranzevia, from a cast R. 4035*g* in the B.M.N.H.

There is a loosely articulated cleithrum in the Gorgonopsid Scylacops according to Broom. The clavicle is a large curved bone articulating with the front edge of the scapula and passing below the interclavicle ventrally.

The interclavicle is a wide flat sheet of thin bone with a pronounced ventral ridge rising to a special elevation.

The only other Gorgonopsid available to me is a cast of the huge Russian Upper Permian Inostranzevia, which differs exceedingly from Scymnognathus.

It has a large thin scapula blade, much curved to surround the animal's thorax, and very broad dorsally. This blade narrows and thickens as it is

traced downwards until it is terminated by the upper part of the glenoid cavity, which appears to be somewhat mutilated. In front of the thick posterior part of the scapula, just above the glenoid region, is a very deep fossa lying on a special thin part of the scapula which projects forwards and whose lower end articulates with the precoracoid.

The coracoid is destroyed, and I am uncertain how much of the edge of the precoracoid is original margin.

Gorgonopsid humeri have been well described by Owen, *Cat. Foss. Rep. S. Africa*, B.M., 1879, pl. xix., *Cynodrakon major*; and by Broom and Haughton in Scymnognathus (*op. cit.*).

The Gorgonopsid humerus is comparatively slender when compared with those described in the preceding part of this paper; it has expanded distal and proximal ends which make an angle of about 30° with one another, so that when the head is placed horizontally the anterior face of the lower end looks downwards and slightly forwards.

The head of the humerus when viewed from the dorsal aspect is straight, the articular surface covering the medial part of its proximal surface commencing abruptly below and extending round so that a little of it is visible on the dorsal aspect of the bone, although from the ventral surface it is quite hidden. From the anterior corner of the head the very powerful delto-pectoral crest runs down the shaft of the bone so that its anterior margin is at right angles to the head. This crest is deep, and stands at a considerable angle to the dorsal surface of the proximal part of the bone, directed downwards. It terminates distally in a smoothly rounded margin continued as a ridge over the entepicondylar foramen to the entepicondylar edge of the lower end of the humerus.

The distal end of the humerus bears on its lower surface towards the ectepicondylar side an almost hemispherical articular condyle for the end of the radius. External to this is the articular face for the ulna, which lies almost entirely on the distal end of the bone. Above the radial condyle a thin extension of the bone forms a very marked supinator crest. This subsides into the dorsal surface of the shaft of the bone, and at its extreme proximal end is perforated by a small ectepicondylar foramen.

Experiment with the bones of Scymnognathus in Cape Town shows that when articulated the humerus stands out from the body so as to lie with its distal end inclining backwards at about an angle of 60° with the animal's principal plane, and with the axis of the bone nearly parallel to the ground. The possible motion lies in a vertical plane.

When articulated in this way the radius and ulna lie side by side and pass down to the ground at an angle which may be about 45°.

Therocephalia.

The only shoulder girdle material yet described is that of Ictidosuchus, which Broom described.

None is available to me; there are in the British Museum, however, a good many scraps of humeri in bad association to Therocephalian skulls, to which they undoubtedly belong. These all resemble the humerus of the fore-limb described by Seeley as Theriodesmus, which certainly belongs to some member of the sub-order.

These humeri seem to be structurally similar to the Gorgonopsid humeri described above, but differ from them in their great slenderness; a difference which extends to all the other limb bones, and shows that as a group the Therocephalia are remarkable for their light build and probably great agility.

Cynodontia.

The Cynognathid shoulder girdle is represented in the British Museum by the magnificent scapulo-coracoid of the type specimen of *Cynognathus crateronotus* (described by Seeley, *Phil. Trans.*, B, vol. 186, pp. 59–148, 1895), which lacks only the lower parts of the coracoid and precoracoid. In addition, the young skeleton of a Cynognathid, described by Seeley as Microgomphodon in error, shows both scapulæ and the anterior margin of a precoracoid identical with those of Cynognathus, and imperfect clavicles and interclavicle.

In South Africa, in the Cynognathus beds of Winnaarsbaaken, Dist. Albert, Cape Province, I collected fragments of a Cynognathid skeleton, including well-preserved but imperfect clavicles, interclavicle, precoracoid and coracoid, and the lower end of the humerus.

There are in the British Museum three perfect and several fragmentary Cynognathid humeri, many exquisitely preserved. As these humeri, of which the largest is twice as long as the smallest, agree exactly in shape, and as there is direct evidence that the proportions of all Cynognathids are similar, I have enlarged the perfect precoracoid of my own specimen to an extent determined from a comparison of the lower end of a humerus belonging to it with the upper end of the humerus of the type specimen of *Cynognathus crateronotus*, thus obtaining a complete scapulo-coracoid.

The scapula is long, broadest at the dorsal end, and during life inclined forward.

The main part of the outer surface forms a deep channel bounded by the everted anterior and posterior margins, which form strong out-

standing ridges. Near its lower end the anterior border is produced into a low and not much thickened acromium. This process does not stand out freely from the bone as in Dicynodon, mammals, and even Embrithosaurus, but is only marked off by the depression of the outer surface of the scapula below it to form a deep fossa, the whole of whose surface

FIG. 8.—*Cynognathus crateronotus*, Seeley, type specimen. Right scapula, with imperfect precoracoid and coracoid, inner surface. × ½.

is visible in a direct lateral view, and which in no way undercuts the acromium; the anterior margin of this fossa is continuous above with the acromium, and below with that of the precoracoid. Although slightly damaged in the type specimen, it is obvious that it was thin and sharp as it is in the little skeleton described by Seeley as "Microgomphodon."

The external surface of the scapula is completed by two small ears arising from the visceral surface of the everted anterior and posterior borders and extending outwards so as to form small anterior and posterior

fossæ at the upper end of the bone. The inner surface of the scapula is saddle-shaped, flat or nearly so dorsally, and very strongly convex in an antero-posterior direction in the middle of its length.

The face with which the precoracoid is articulated is short, straight, and fairly thick.

The precoracoid of the Winnaarsbaaken specimen, which is very well preserved, has separated from the scapula at its suture. It is a small bone, perforated at about the middle of its length, but near to its suture with the

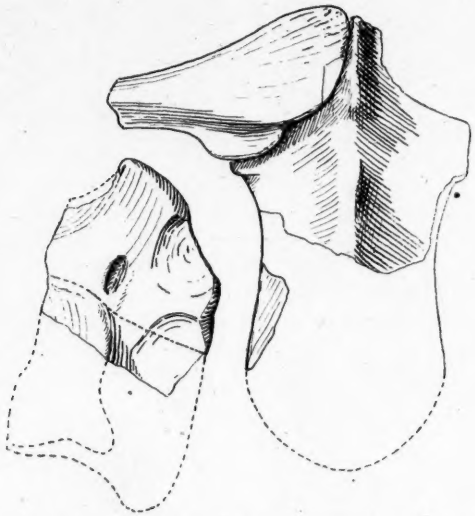

FIG. 9.—Cynognathid, ? gen. Right precoracoid and fragment of coracoid, lower end of right clavicle, and interclavicle. From the Cynognathus zone of Winnaarsbaaken, Dist. Albert, Cape Province, S. Africa. $\times\frac{2}{3}$.

coracoid, by a rather large foramen. It extends forwards some way in front of the suture with the scapula; this margin is somewhat damaged proximally, but shows by its rapid thinning that not more than two millimetres can be missing. The perfect distal part supports this conclusion.

The ventral margin of the bone forms nearly a quadrant of a circle, and is raised into two distinct thickenings, from each of which a ridge runs on to the outer surface of the bone; these thickenings are sharp-edged, and agree exactly in character with those on the dorsal edge of the scapula of an old adult Echidna.

On the inner surface the foramen through the precoracoid ends in the

lower extremity of a small deep fossa lying on both precoracoid and scapula.

The coracoid is nearly completely preserved in the type specimen, its anterior part also in the Winnaarsbaaken specimen. It is much larger than the precoracoid, and has a long, bent suture with the scapula. The outer surface of the coracoid is much more extensive than the inner, and the suture with the precoracoid is not at right angles to the surface.

The glenoid cavity is carried entirely by the scapula and coracoid; the upper part on the former bone faces outwards and downwards at an angle of about 45°, the lower half of the cavity facing nearly directly outwards. Both are nearly flat, and have no curvature in an antero-posterior direction.

The lower end of the right and what is probably the upper end of the left clavicle are well preserved in the new specimen.

The upper end is bent to form a quadrant of a circle; its lower end is circular in section, whilst the upper end is flattened in the plane of the curvature of the bone and ridged for attachment to the acromium. The lower end is nearly straight, and gradually widens from its cylindrical shaft. This part of the bone rests on the lower surface of the anterior part of the interclavicle.

The interclavicle is represented by its perfect anterior end, connected by matrix with a part of the right lateral border so as to give the shape of most of the posterior part.

The bone forms a thin slightly concavo-convex plate with a pronounced ridge down the middle line of its ventral surface.

Anteriorly the bone ends in a narrow massive rod of triangular section, whose lateral margins suddenly widen to form short blunt lateral processes, to which the clavicles are attached. Between these processes the median ridge is lowered so as to form a transverse groove, behind which it rises to a summit from which it steadily descends posteriorly. The posterior part of the bone is very wide, nearly as much across as the two clavicular arms.

The humerus generally resembles that of the Gorgonopsia, but presents some differences of importance. The head is expanded, the articular surface occupying the middle of it; anteriorly the deep delto-pectoral crest rises from its lower surface; caudally it ends in a thickening covered with muscle insertions. The cylindrical articular surface of the head does not extend on to the ventral surface, but is largely exposed in dorsal view. The proximal part of the shaft of the bone is flattened, with a concave ventral surface bounded on the outer side by the powerful delto-pectoral crest so as to form a very broad bicipital groove. The dorsal surface is rounded, and is crossed obliquely by two grooves which mark the insertion of the lateral humeral head of the triceps and the brachialis internus.

The delto-pectoral crest is long, and its distal end subsides abruptly into the shaft, being continued by a ridge which forms the bar across the entepicondylar foramen and runs on to the inner margin of the expanded lower end of the humerus.

The lower end of the humerus is expanded, its broad plane lying nearly parallel to that of the head. The radial condyle is confluent with

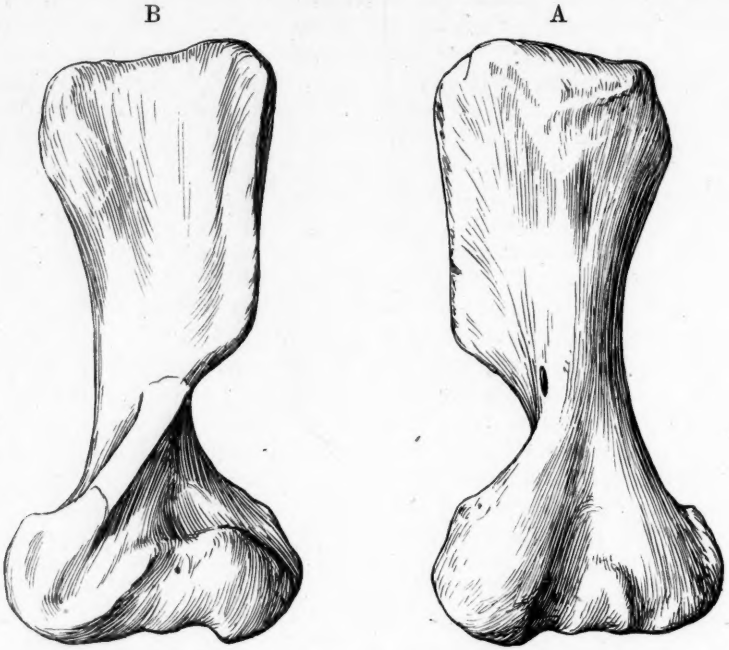

FIG. 10.—Left humerus of a Cynognathid. Dorsal (A) and ventral (B). × ½.

that for the ulna, and forms a cylindroidal surface lying almost entirely on the lower face of the bone.

The ulna articulation is extensive; on the front face it is confluent with that for the radius, but does not extend so far proximally. It passes over the distal end of the humerus on to a rounded boss on the dorsal surface.

The ectepicondylar region is thick and massive, and gives origin only to a small supinator crest. There is a small ectepicondylar foramen perforating the dorsal surface of the shaft at about the level of the lower end of the deltoid crest.

Normal Position.

Actual experiment with the perfectly preserved scapulo-coracoid of Cynognathus and consideration of the shape of the lower border of the precoracoid and coracoid have convinced me that the Cynognathid shoulder girdle leant forward at the top just as does that of Echidna. When placed in what is obviously its natural position, the glenoid cavity looks outwards and backwards. The shape of the head of the humerus, and especially the great production of its articular surface on to the dorsal surface, show that normally it was carried parallel to the ground. The obliquity of the head on the shaft makes the plane containing the humerus in its normal position lie at about 45° to the animal's principal plane—that is, its elbows are only slightly turned out. The cylindrical shape of the humeral articulation shows that the bone can have had freedom of motion only in the vertical plane.

When the humerus is placed in its normal position, the expanded lower end lies very nearly parallel to the ground.

Unfortunately, I have no bones of the fore-limb. The articulations for them on the humerus suggest that these bones had considerable range of motion in the plane including the long axis of the humerus and standing at right angles to its expanded lower end.

The series of Cynognathid humeri at my disposal show nearly all the muscle insertions clearly in one or other specimen; all that are clearly determinable are represented in fig. 11. The determination of these muscles depends on a comparison with the Pelycosaur humerus described in an earlier part of this paper, which itself agrees with Sphenodon and with Echidna.

It seems unnecessary to describe these insertions in words.

Knowing the insertions of the shoulder muscles on the humerus, we are in a position to investigate the musculature of the scapulo-coracoid, in which the insertions are not very clearly shown. It is at once obvious that the great concave external face of the scapula gives origin to the scapulo-humeralis anterior, whose humeral insertion lies immediately below the lower end of the groove. There is a very marked insertion for the scapula head of the triceps in the form of a narrow crest on the posterior face of the scapula just above the level of the top of the glenoid cavity.

The scapulo-humeralis posterior lies caudal to the scapula head of the triceps, and arises from the posterior and medial surface of the great posterior crest forming the posterior side of the deep groove on the outer face of the scapula; it no doubt extends up to the top of the bone in front

of the little posterior wing which extends the area for the insertion of the serrati.

Professor Seeley and all subsequent authors have held that the anterior wing of the scapula forms a mammalian prespinous fossa occupied by a supraspinatus muscle running downwards under the clavicle below the acromium to be inserted on the head of the humerus just in advance of the articular condyle.

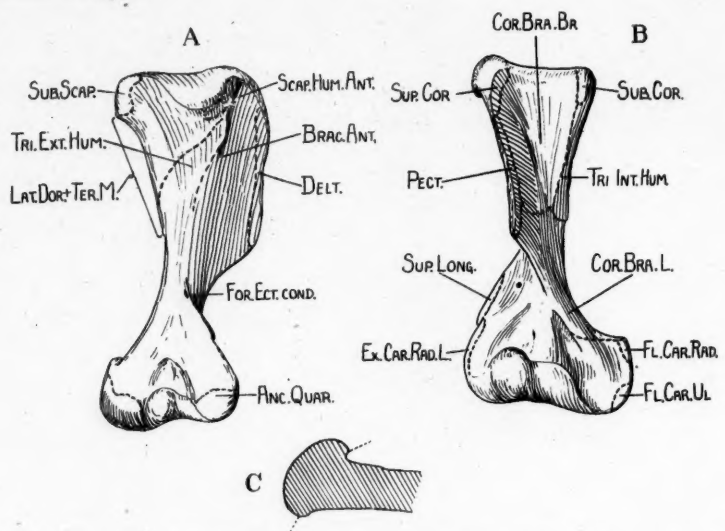

FIG. 11.—Right humerus of a Cynognathid, ? Diademodon. $\times\frac{2}{3}$. On these drawings I have indicated by thick dotted lines the muscular insertions visible on all the specimens of this bone available, (A) dorsal, (B) ventral aspects. Reference letters as before, with :—

Anc. Quar., anconeus quartus origin ; Ex. Car. Rad. L., origin of extensor carpi radialis longus ; Fl. Car. Rad., flexor carpi radialis origin ; Fl. Car. Ul., origin of flexor carpi ulnaris ; For. Ect. Cond., ectepicondylar foramen ; Sup. Long., origin of supinator longus. C, section of the head along the axis, to show the articular surface, included between the two dotted lines.

This view seems to me to be mechanically impossible, for it would involve the muscle or its ligamentous continuation gliding over the slightly concave margin of the scapula below the acromium and very markedly changing its direction at this point; as this margin is exceedingly thin and sharp-edged, it seems incredible that it ever did act as a gliding surface in this way. In any case, the fact that, although smaller, the caudal wing of the scapula is exactly similar to the anterior wing, suggests that this latter expansion has arisen to provide attachment for a large omotrachelian or (and) anterior part of the serratus series.

The deep fossa below the acromium on the outer surface of the scapula I hold to have been occupied by a separated part of the scapulo-humeralis anterior, just as the very similar fossa in Inostranzevia undoubtedly was. An obscure ridge on the visceral surface of the scapula, running from above downwards and backwards at about the middle of the bone, seems to mark the insertion of the subscapularis, whose principal insertion may have been on the anterior and inner surface of the outwardly reflected anterior margin of the scapula, the muscle winding round the inner surface of the bone and passing directly downwards to its insertion on the dorsal surface of the lesser tuberosity of the humerus.

The supracoracoideus was obviously inserted in the whole free border of the external face of the precoracoid, and ran directly to its insertion into the proximal part of the ventral surface of the delto-pectoral crest.

The coraco-brachialis had an insertion just as in Echidna or Sphenodon.

Mode of Walking.

It is most convenient to discuss the action of the shoulder musculature in two parts, first keeping the fore-arm fixed nearly at right angles to the humerus.

With the bones in this position and the animal standing on its two hind-legs and the left fore-leg at its extreme backward position, the right humerus is depressed by the action of the coraco-brachial and pectoral muscles. Owing to the shape and position of the glenoid cavity, this drives its lower end forwards and inwards so that the hand approaches the animal's middle line well in advance of the glenoid cavity. If the hand be now placed on the ground, the action of the scapulo-humeralis anterior, scapulo-humeralis posterior, latissimus dorsi, and to a less extent the deltoid and subscapular muscles, raising the humerus, will not only raise the animal but drive it forwards and to the left side. At a certain point of this motion, when the hand is vertically under the glenoid cavity, the animal will be balanced on this limb; if the motion continues, the pectoral and coraco-brachialis come into strain as the animal, as it were, falls forward. If now, by the action of the triceps, the fore-arm is extended on the humerus, the animal is still urged in the same direction, and further depression of the humerus will bring the arm to its extreme backward position. At this stage the left arm is advanced and repeats the motions above described, while the right hand is picked up by the action of the extensors, brachialis anticus, biceps, etc., the fore-arm flexed, and the humerus driven forwards by the coraco-brachialis, pectoral, deltoid, and supracoracoideum.

Thus in this type of walk all the muscles proceeding from the animal's body to the humerus are actually used at one stage or another to drive the

animal forwards, none serving solely for support or to oppose rotational couples produced in the humerus by the action of the fore-limb musculature.

Dicynodontia.

The Dicynodonts are a side branch of the mammal-like reptiles, very specialised in their skull structure, and leading to no other group. Their

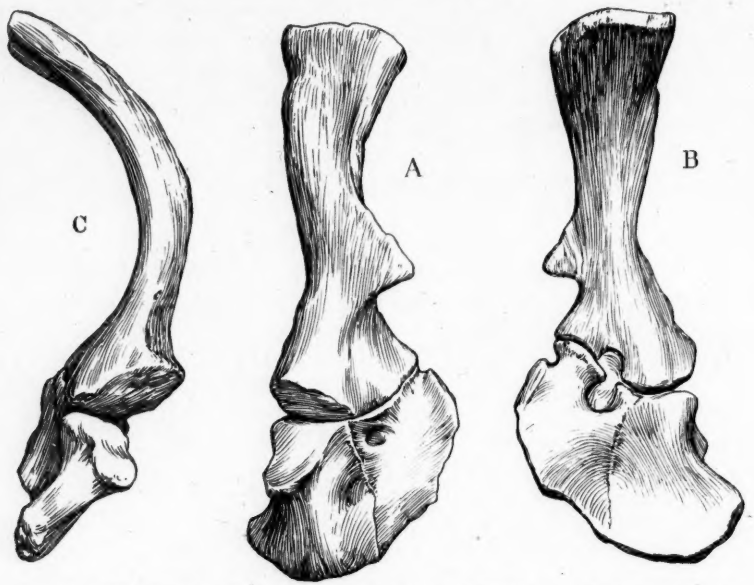

Fig. 12.—Right scapula, coracoid, and precoracoid of *Dicynodon halli*, Watson, from the outer (A), inner (B), and posterior (C) aspects. From the type specimen. $\times \frac{1}{3}$.

shoulder girdle and fore-limb are, however, of great importance, because in them for the only time in known reptiles we get a typical supraspinous muscle of Monotreme type. The group has a long history, and slight changes of proportion and of the position of the humerus take place within it.

Dicynodon is best represented by the type skeleton of *D. halli*, Watson, found by the writer in the lower part of the Cistecephalus zone at Kults Poort, Dist. Beaufort West. The bones of this individual are magnificently preserved and undistorted, with the exception of one clavicle and of a notch in the lower border of one coracoid formed by the pressure of a humerus which lay on it. All the bones of the fore-limb were heaped

together, the right radius and ulna being naturally articulated at right angles to the broad surface of the lower end of the humerus, and standing up perpendicular to the bedding of the rocks.

The scapula has a slender blade, very much curved in a transverse plane so as to fit over the rounded body of the animal. The blade is throughout thick, but becomes more massive at the lower end, where it furnished the upper half of the glenoid cavity.

The anterior margin of the scapula is produced directly forwards into a slender acromium, which is terminated below by a margin continued by a definite ridge on to the outer face of the bone. Below the acromium the scapula extends forwards so as to form the articulation for the precoracoid. The conditions are such that the plane of the surface of this part of the scapula if continued upwards passes below the acromium so as to leave a smoothly rounded groove leading downwards from the inner face of the scapula to the outer surface.

The anterior margin of the scapula above the acromium forms a flat roughened face, directed forwards, with which the cleithrum articulated.

The anterior part of the lower face of the scapula presents a flat surface with which the precoracoid articulates; this margin on the inner side is crossed by a deep small depression which continues the fossa on the visceral surface of the precoracoid into which the foramen piercing that bone opens.

The posterior part of the lower end of the scapula is divided into two parts—a small inner face with which the coracoid articulates, and a much larger area facing downwards, backwards, and outwards, which is the upper part of the glenoid cavity.

The precoracoid is a small square nearly flat bone which articulates by straight sutures with the scapula and coracoid. Near the junction of these sutures the bone is perforated by the precoracoid foramen, which opens into a small deep fossa on the inner surface.

The outer surface of the bone is shallowly concave; the inner surface is similarly concave but is crossed obliquely by a low broad ridge.

The coracoid articulates by a long close suture with the precoracoid and by a short loose articulation with the scapula; its outer surface bears the lower glenoid surface, looking upwards and outwards and carried backwards by a special outstanding process.

The cleithrum is not preserved, but was undoubtedly a slender slip of bone, articulated with the whole anterior border of the scapula above the acromium.

The perfectly preserved right clavicle is a slender bone with a round shaft bearing a sharp ridge along its caudal surface. The lower end of the

bone is slightly expanded, its inner surface being recessed to receive the ridge on the interclavicle with which it articulates. The upper end of the clavicle is expanded in a plane at right angles to the lower so as to rest on the outer surface of the acromium, and undoubtedly also to a large extent on the lower end of the cleithrum. Its inner surface is excavated so as to clasp the bones with which it articulates.

The anterior part of the interclavicle is preserved: it forms a wide flat plate with a ridge along the middle line of its ventral surface and two low ridges starting from this and passing out at right angles. These give attachment to the clavicles, which nearly meet in the middle line. So far

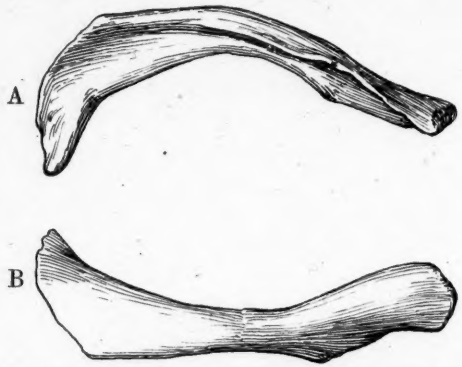

FIG. 13.—Right clavicle of *Dicynodon halli*. A, from behind, lower surface upwards, scapula end to the left. B, ventral surface, anterior border upwards. ×⅔.

as preserved, the bone is extremely similar to that of a Cynognathid illustrated in fig. 9.

The sternum is not preserved, but in the very closely allied *D. microtrema*, Seeley, is a hexagonal plate quite similar to that ascribed by Owen (*Q.J.G.S.*, vol. xxxvi. pp. 414–424, pls. xvi. and xvii.) to Platypodosaurus.

Material of *D. microtrema* shows exactly the mode of articulation of the clavicle with the scapula and the relation of the coracoid to the sternum.

If the scapulo-coracoid of *D. halli* is placed with the ventral edge of the precoracoid and coracoid parallel to the middle plane of the animal, the upper end of the scapula is thrown forward exactly as in Echidna and Ornithorhynchus; that this position is the normal one is shown at once by articulating the clavicle, whose connections at both ends were

certain. It is quite impossible to place these bones in any other position so as to give a possible form to the animal's neck and thorax.

That this position is the normal one in Dicynodonts is shown by numerous skeletons still connected by matrix, in which the upper end of the scapula always lies far in advance of the lower.

The humeri of *D. halli* are perfectly preserved. They have expanded upper and lower ends at an angle of about 60° with each other.

FIG. 14.—Left humerus of *Dicynodon halli*. $\times \frac{2}{3}$.

Viewed ventrally the head is straight, only its middle portion being occupied by the articular surface, which is scarcely visible in this view, but which extends well over into the dorsal surface.

From the anterior end of the head the enormous delto-pectoral crest is developed as a flat plate standing nearly vertically when the skeleton is naturally articulated. The posterior end of the head is thickened to form a powerful lesser tuberosity from which a strong muscular ridge runs down the inner side of the bone to terminate in a large well-roughened process for the insertion of the latissimus dorsi and scapulo-humeralis

posterior. The shaft is short and thick, crossed on its ventral surface by a ridge which continues the lower extremity of the pectoral crest and extends on to form the bridge over the entepicondylar foramen.

The expanded lower end of the bone bears on its front (ventral) surface a small round but flattened condyle for the head of the radius. The ulna condyle lies very largely on the end of the bone, but extends on to both

Fig. 15.—Right radius and ulna of *Dicynodon halli*.
A, humeral ends, radius on the right. B, posterior surface. × ⅔.

broad surfaces. The ectepicondyle is massive, and bears on the sharp outer edge a very distinct process for the origin of the supinator longus. The entepicondyle is of considerable size, but presents no interpretable traces of muscle insertion.

The radius is a straight slender bone with a slight concavity on its proximal end which fits the flattened condyle on the humerus.

The ulna is a still more slender bone, whose expanded upper end lies partly behind the radius and is divided into two parts—the outer formerly continued by cartilage to form an olecranon, the inner articulating with the condyle on the humerus.

The bones of *D. halli* and closely allied species at my disposal do not

show muscular insertions sufficiently clearly to demand a detailed discussion, but give evidence that the whole arrangement agreed in its general structure with Cynognathus One feature, however, of great importance is that there must have been a distinct though small supraspinatus inserted on the inner surface of the scapula and passing downwards over the

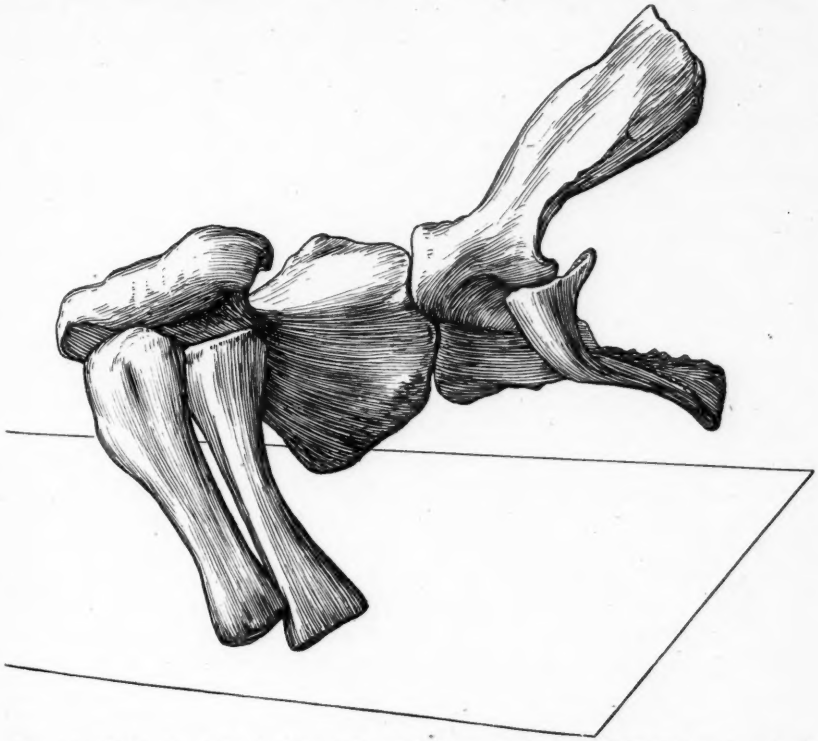

FIG. 16.—Right side of the shoulder girdle and fore-arm of *Dicynodon halli*, Watson, in natural position, from the type specimen. The specimen stands on a rectangular surface, the hinder edge of which is under the animal's middle line. $\times \frac{2}{3}$.

smooth notch below the acromium to be inserted on the greater tuberosity, which lies just below.

The bones of *D. halli* are so well preserved that there is no difficulty in articulating them and studying their movements.

When the shoulder girdle is in its true position, the humerus in its extreme anterior position (fig. 16) stands out nearly at right angles to the body and lies with the outer end of its axis pointing upwards.

The fore-arm stands at right angles to the broad plane of the lower end of the humerus, coming down to the carpus at an angle of about 45° with the ground.

The flat radial condyle suggests that the possible amount of flexion and extension of the fore-arm was small, and I think that there is little or no motion possible in a plane at right angles to this.

The humerus can be moved only in one plane, or at any rate its possible motion out of this plane can only be very small, so that it can be depressed and moved backwards, through a considerable arc, at about 45° to the ground. Such motion raises and drives forward the animal, and a flexion of the fore-arm at the same time throws the animal towards the side considered, sufficiently to get the centre of gravity within the triangle formed by this fore-foot and the two hind-feet. The very short fore-arm and its limited motion on the humerus suggest that the fore-foot never actually lay below the animal's body, and that as a measure for increasing the stability the hind-foot of the opposite side was in its most advanced position when the fore-foot was retired.

The order of putting the feet down would be: left fore, left hind, right fore, right hind. Consideration of these possibilities suggests that the track was wide and the stride fairly long. Fortunately, we have actual tracks which were in all probability made by Dicynodonts.

In the Cutties Hillock beds (Upper Permian) of Elgin, Scotland, which have yielded a large number of individuals of the Dicynodont Gordonia and Geikiea, whose skulls and fragmentary skeletons agree with the South African Dicynodons such as *D. halli* in all important features, I found a fore and hind footprint of a form which is represented by numerous well-preserved tracks in the Cummingstone beds of the neighbourhood and in numerous other localities in Britain. For a description and figures of these tracks see H. G. A. Hickling, *Manchester Memoirs*, vol. liii. No. 22, pls. i.–iv.

The footprints of these tracks are short, five-fingered and clawed, quite similar to those which should be made by Dicynodon feet (*cf.* Owen, *Q.J.G.S.*, vol. xxvi. pl. xvii. fig. 5).

The tracks are wide, the prints of the feet of opposite sides being distant from each other, and the stride as long as the width of the track; the smaller hind footprints often follow closely on the fore footprints of the same side, and the whole agrees very closely with the type of walk inferred from the characters of its bones to have been used by Dicynodon.

In fig. 17 I have illustrated the scapulo-coracoid, interclavicle, and sternum of a small Dicynodon from the Endothiodon beds of Beaufort

West. In this individual the scapula is even more markedly inclined forward than in *D. halli*, and the precoracoid is considerably bigger, both relatively to the scapula and to the coracoid.

The complete interclavicle is unusual in its considerable contraction behind the arms which give attachment to the clavicle, agreeing in this feature with other interclavicles of small Dicynodons from the same beds, and differing from the larger later forms.

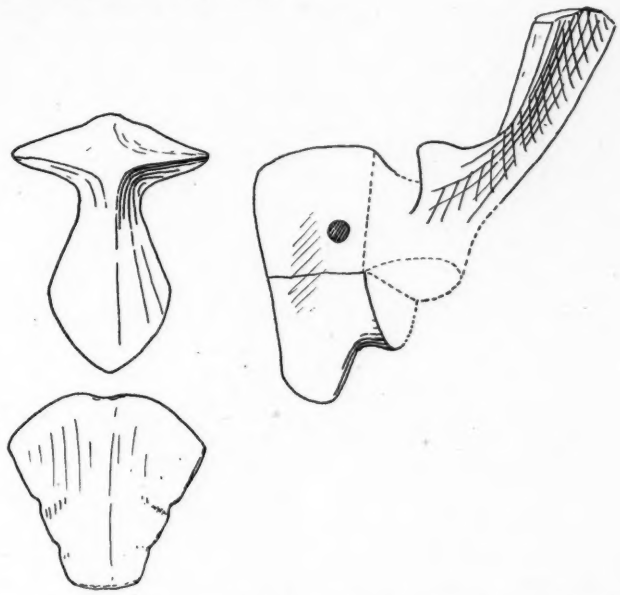

FIG. 17.—Left scapulo-coracoid, interclavicle, and sternum of a small Dicynodon from the Endothiodon zone of Beaufort West. ×1.

The sternum is a single pentagonal element giving evidence of the attachment of two sternal ribs, but otherwise a mere flat plate. Several specimens of large and small forms give definite evidence that it was not followed by any other ossified sternal element.

The very large Dicynodont Kannemeyeria, from the Cynognathus beds (Lower to Middle Trias) of South Africa, is represented by splendid material in the British Museum, from which I have drawn a few bones in figs. 18 and 19.

Its shoulder girdle on the whole resembles that of *D. halli*, but the notch below the acromium for the supraspinatus is better developed, and

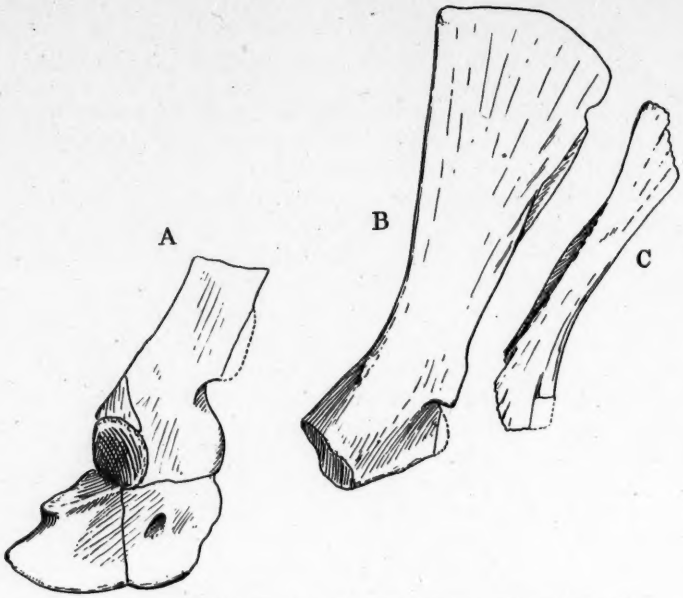

FIG. 18.—*Kannemeyeria* sp. A, right scapula, precoracoid, and coracoid. B, right scapula. C, right cleithrum. ×$\frac{1}{5}$.

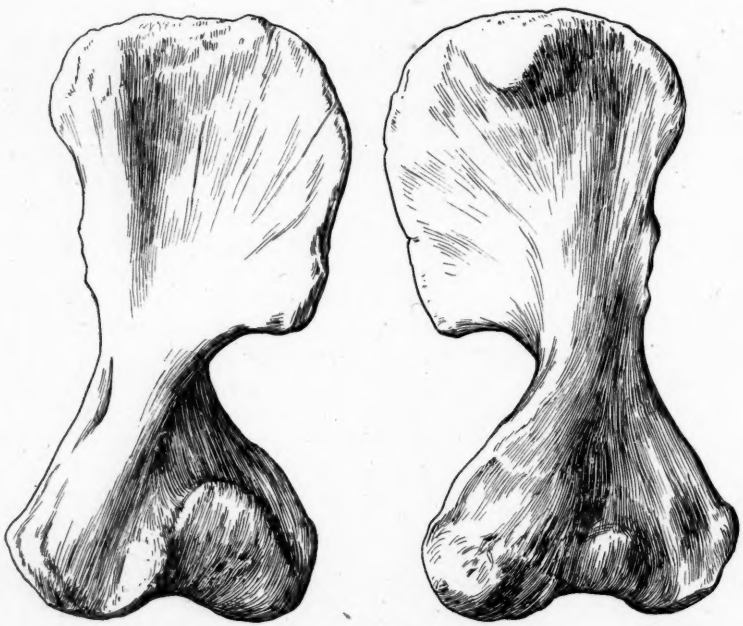

FIG. 19.—*Kannemeyeria simocephalus* (Weithofer). Left humerus. ×$\frac{1}{4}$.

the precoracoid and coracoid are smaller in proportion to the scapula and the coracoid larger when compared to the precoracoid.

The glenoid cavity faces very much more directly backwards than in *D. halli*, the articular face on the coracoid lying almost entirely caudal to the scapula.

The humerus generally resembles that of *D. halli*, but differs in the narrower lower end and in the much more extended and better rounded condyle for the radius, and in the fact that the expanded ends lie much more nearly in one plane, being placed at an angle of about 30°. The bones of the fore-limb are similar to those of *D. halli*.

There is no doubt that in Kannemeyeria the humeri did not project so strongly from the animal's body as in the earlier form, and that in consequence the walk more nearly resembled that of Cynognathus.

Lystrosaurus.

The aquatic Dicynodont Lystrosaurus much resembles Dicynodon itself in all the bones of the shoulder girdle and fore-limb, but is remarkable, at any rate in some species, for the very large size of the supraspinatus notch below the acromium.

Monotremes.

The shoulder musculature of the Monotremes has been repeatedly described, best by W. J. S. M'Kay (*Proc. Linn. Soc. N.S.W.*, vol. ix., 1895, pp. 263–358, pls. xx.–xxiii.), who reviews all previous work. The morphology of the shoulder girdle was discussed by J. T. Wilson and M'Kay (*Proc. Linn. Soc. N.S.W.*, vol. viii., 1894, pp. 377–387, pl. xxi.), who cleared up the whole problem of the homologies of the borders and surfaces of the scapula with those of an ordinary mammal in a clear and convincing manner. I wish especially to express my indebtedness to this paper, which first led me to the views of muscle homologies which are adopted in this paper. The most significant features are:—

That there are epicoraco-brachial and epicoraco-humeral muscles attached to the anterior coracoidal element which are unrepresented in other mammals; that the long head of the biceps is attached to the same bone; that the spine and acromium form the front edge of the scapula, the insertion of the supraspinatus being entirely on the inner surface; and that the subscapularis arises largely from the outer surface of the scapula.

C. Westling (*Bihang till K. Afd. Svenska Vet.-akad. Handlinger*, Bd. xv. Afd. iv. No. 3, pp. 3–71, pls. i.–vi.) gives good figures of the humerus of Echidna with the muscle insertions marked.

Trichosurus.

R. Broom in 1899 made the very interesting discovery that in small pouch young of Diprotodont marsupials the coracoid extended inwards as a large cartilage and finally became continuous with the sternum. Subsequently he published an illustrated account of the development of the shoulder girdle in these animals, with many graphical reconstructions from serial sections. Later he discussed the Polyprotodonts. Although examination of series of embryos completely confirmed Broom's results, I thought it would be interesting to see the structures concerned in the solid and to get further

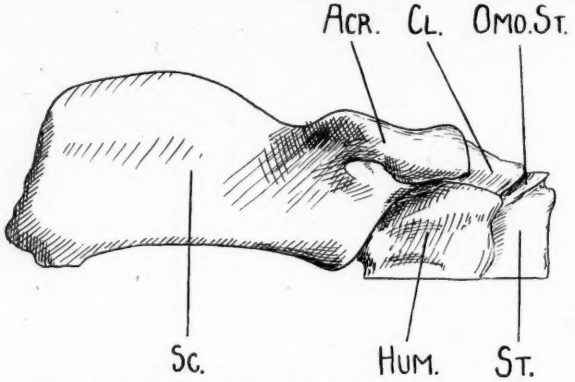

Fig. 20.—Wax-plate model of the shoulder girdle of an 11·5-mm. Trichosurus embryo. Right side of the shoulder girdle from without. ×33.

Acr., acromium; Cl., clavicle; Hum., head of humerus; Omo. St., omosternum; Sc., scapula; St., sternum.

light on the musculature. I therefore made a wax-plate model of an 11·5-mm. embryo of *Trichosurus vulpecula* from one of Professor J. P. Hills' series. In this model, which is illustrated in figs. 20 to 24, the skeletal structures are shown on the right side and the shoulder musculature (except the rhomboid) on the left.

The upper end of the scapula lies opposite the last three cervical and first dorsal vertebræ; it inclines very slightly backwards as in the adult.

The blade of the scapula is a thick sheet of cartilage of considerable breadth, with a concave inner surface and an outer surface bevelled off to the anterior margin, and with a slight concavity on the middle of its face. Ventrally the scapula narrows, and from its anterior margin above the glenoid cavity the very large hook-shaped acromium arises by a narrow neck. The acromium is at first directed outwards, then turns downwards,

and finally points inwards; it is throughout a thick rod, and lies in a transverse plane of the animal. The lower end of the scapula turns towards the middle line, having a massive tuberosity overhanging the glenoid cavity, into which the ligamentous long head of the biceps is inserted. The coracoid is a quite massive cartilage, with a low prominence

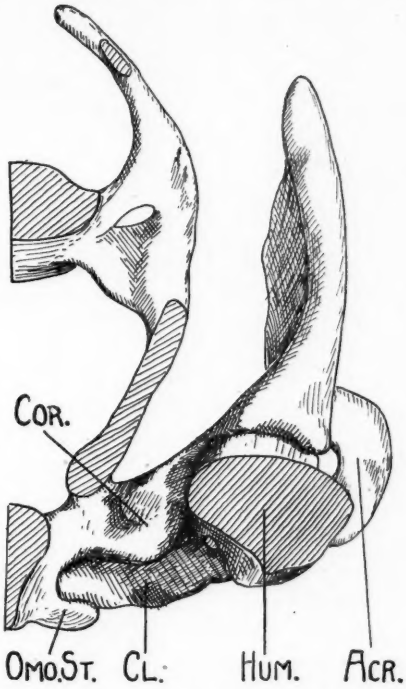

FIG. 21.—Trichosurus as in fig. 20. Right side of the shoulder girdle from behind. Reference letters as before, with :—

Cor., coracoid.

on its caudal surface just medial to the inner lip of the glenoid cavity. The inner end of the coracoid is in wide cartilaginous connection with the sternum and first dorsal rib. The glenoid cavity is concealed by the head of the humerus in the model and is still not completely formed, the split separating it from that element being not yet carried through; it is a large shallow concave area facing downwards, backwards, and outwards.

The sternum is a massive cartilage whose lateral borders fuse with

the coracoid and first rib, behind which the width is very much reduced, so that the presternum forms a pronounced knob.

The clavicle is already considerably ossified and shows no trace of cartilage, consisting only of dense connective tissue. It takes the form of a nearly straight rather massive rod, the tissue of which it is composed

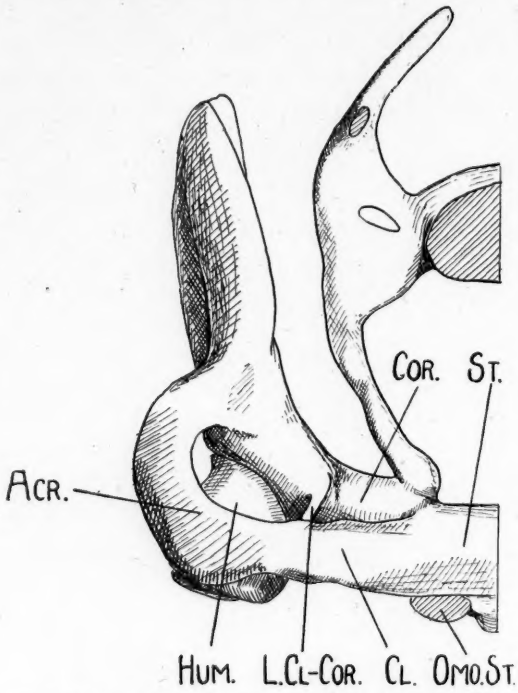

FIG. 22.—Trichosurus as in fig. 20. Right side of the shoulder girdle from in front. Reference letters as before, with :—

L. Cl. Cor., coraco-clavicular ligament.

being continuous with the perichondrium of the acromium at one end and that of the sternum at the other.

The omosternum at this stage and in the embryo from which the model was made consists entirely of dense connective tissue exactly similar to that of the clavicle. It forms a small triangular patch with straight anterior surface lying over the inner ends of the clavicles and sternum. Anteriorly it is very markedly separated from these elements by deep slits passing inwards from its lateral sides (*cf.* fig. 25), but

posteriorly it becomes continuous with the thick perichondrium of the ventral surface of the sternum.

In another embryo of the same size (11·5 mm.) it still contains no trace of cartilage, but does show the very beginnings of ossification in two points of its antero-lateral regions.

The humeri are still entirely cartilaginous, being of course much shorter and thicker than in the adult. They stand directed backwards and outwards, and with their distal ends more dorsally placed than the proximal. The head is large, rounded, and faces very largely dorsally,

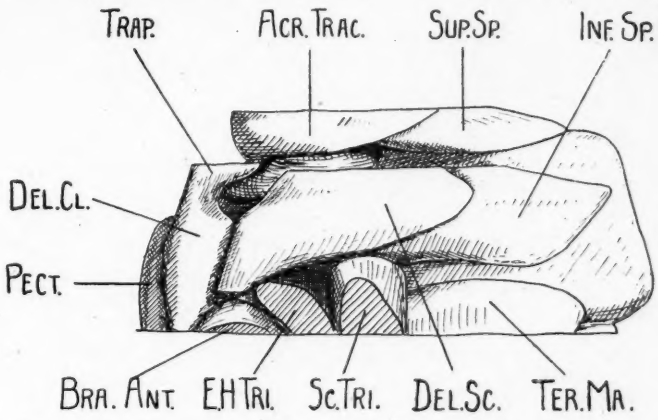

FIG. 23.—Trichosurus as in fig. 20. Left shoulder musculature from outside. Reference letters as before, with :—

Acr. Trac., acromio-trachealis ; Del. Cl., clavicular deltoid ; Del. Sc., scapular deltoid ; E. H. Tri., external humeral head of triceps ; Inf. Sp., infraspinatus ; Pect., pectoralis ; Sc. Tri., scapular head of triceps ; Sup. Sp., supraspinatus ; Ter. Ma., teres major ; Trap., trapezius.

the greater and lesser tuberosities being well marked and much separated so as to leave a wide shallow bicipital groove.

Musculature.

So far as they are represented in the model, the serrati arise from the tips of the parapophyses of the 4th, 5th, 6th, 7th cervical vertebræ just outside the vertebraterial canal and from the outer margin of the proximal part of the first dorsal rib; how far backwards they extend I have not determined. They rapidly approach one another, forming a single sheet of muscle which is inserted into the dorsal part of the perichondrium of the front edge of the scapula, into the inner surface of

that cartilage just below its dorsal border, and into the connective tissue covering its caudal edge.

The omohyoid muscle is a thin strip passing under the serrati and inserted into the visceral surface of the scapula ventral to the insertion of these muscles.

The acromio-trachelian is a powerful muscle inserted into the anterior surface of the outer part of the acromium and widening rapidly as it passes forward over the supraspinatus.

The trapezius is a thin sheet inserted into the ventral surface of the clavicular end of the acromium, some of its outer fibres extending on to become continuous with the clavicular deltoid.

The cleido-mastoid and cleido-occipital are small muscles of circular section inserted into the front surface of the middle of the clavicle.

The sterno-mastoid is a large muscle arising entirely from the lateral part of the front face of the omosternum.

The subclavius is a single flattened muscle arising from the first dorsal rib just dorsal to its fusion with the coracoid, and passing directly forward over the coracoid and scapula to be inserted into the extreme outer end of the clavicle and into the fascia surrounding the supraspinatus as it plunges under that bone.

Two or three parts of the pectoralis major are shown in the model. The first arises from the median line of the ventral surface of the sternum and omosternum, and passes outwards to join the lateral clavicular part. The second part is really only composed of the partially separated deep layers of the first. The third arises from the outer end of the clavicle, and faces backwards and outwards, becoming continuous with the first until finally they are all inserted into the pectoral crest of the humerus.

The pectoralis minor is a small muscle arising from the ventral surface of the coracoid and passing almost directly backwards to its insertion into the posterior part of the sternum. Throughout it lies deep to the pectoralis major.

The clavicular deltoid arises from the lower part of the acromium, and is continuous with some of the outer fibres of the trapezius; it passes from here directly backwards to the humerus.

The scapular deltoid arises from the thick sheet of connective tissue which joins the acromium and separates the supra- and infraspinati. It lies over the latter muscle, and runs downwards and backwards to its humeral insertion.

The supraspinatus arises from a very small area of the outer surface, from the anterior margin and largely from the inner surface of the blade of the scapula. It passes downwards between the acromium and the

glenoid part of the scapula to be inserted on the outer tuberosity of the humerus.

The infraspinatus has its origin from the outer face of the blade of the scapula, and passes downwards caudal to the acromium to its insertion near but dorsal to the supraspinatus on the great tuberosity.

The teres major is a thick muscle having its origin from the extreme posterior strip of the outer face of the scapula and the posterior edge of that cartilage. It passes downwards caudal to the scapular head of the triceps, and with its inner side in contact with the subscapularis and serratus.

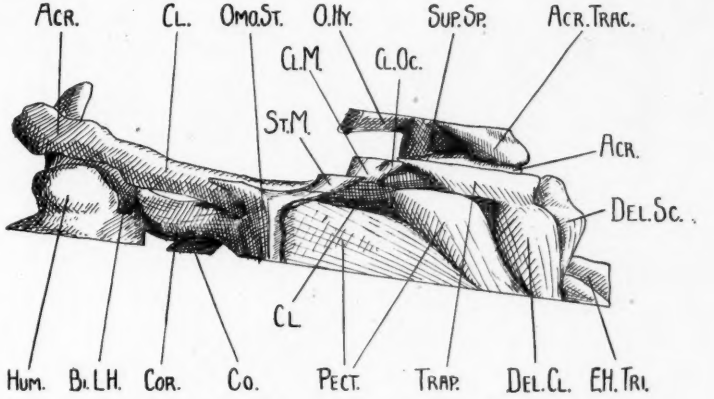

Fig. 24.—Model of Trichosurus as in fig. 20. Shoulder girdle and left shoulder musculature from below. Reference letters as before, with :—

Bi. L. H., long head of biceps tendon ; Cl. M., cleido-mastoid ; Cl. Oc., cleido-occipital ; Co., 1st dorsal rib ; O. Hy., omohyoideus.

The sub-scapularis arises from the inner surface of the scapula below the omohyoideus and serrati and behind the supraspinatus. It lies dorsal to the subclavius, and finally winds round over the glenoid region of the scapula to its insertion into the lesser tuberosity.

The biceps arises by a long ligamentous head from the tuber of the scapula in front of the glenoid cavity and from the process in the caudal surface of the coracoid. The two parts soon meet and have their usual course.

The coraco-brachiales, brevis and longus, arise near the coracoid head of the biceps from the posterior and dorsal surface of the coracoid, and cross that bone in their course to be inserted into the lower surface of the humerus.

The triceps and brachialis anticus present no feature of special interest

except that their insertions extend well up to the head of the humerus. There is a well-marked coraco-clavicular ligament connecting the anterior face of the scapula, where it passes into the coracoid, with the outer end of the clavicle. There are no traces of subcoracoid or supracoracoid muscles.

I have confirmed Broom's account of the breaking down of the inner end of the coracoid into a ligament in older individuals of Trichosurus.

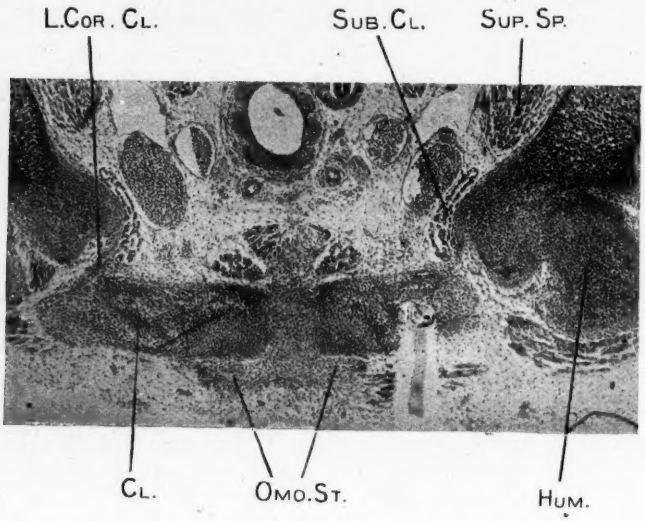

Fig. 25.—Photograph of a transverse section of an 11·5-mm. Trichosurus, to show the distinctness of the omosternum. Reference letters as in preceding figures.

In a preparation of a much larger embryo (18 cm.), which Mr Tan was good enough to make for me, the ligament passes from the end of the coracoid to the outer edge of the presternum just in front of the insertion of the first rib. The cartilaginous coracoid is still quite large, forming half the glenoid cavity, and contains a single bone.

Discussion of the Evidence presented in the foregoing Pages.

The chief outstanding problems of the shoulder girdle of the animals discussed in this paper are:—

1. Are the clavicles of a mammal strictly homologous with those of Labyrinthodontia?

2. What is the fate of the interclavicle in Theria?
3. Which of the two coracoidal elements of Cynognathus is the mammalian coracoid?
4. Is the "epicoracoid" of the Monotreme shoulder girdle homologous with the anterior coracoidal element in early reptiles, or is it a neomorph corresponding to the "epicoracoid" of a lizard?
5. With what muscles of a reptile do the supra- and infraspinati and teres major of a mammal correspond?

1. The doubt whether the mammalian clavicle is homologous with that of reptiles was first introduced by Gegenbaur, who was a profound believer in the hypothesis that if two bones developed, one in cartilage and the other in membrane, they could not be homologous. Gegenbaur found that in man the clavicle develops in cartilage, and hence argued that it could not correspond solely with a membrane bone of dermal origin such as the clavicle of the lower Tetrapods was known to be, but must also include a vestige of the old Urodele precoracoid.

Broom (1899, *Trans. Roy. Soc. Edin.*, vol. xxxix. pl. iii. No. 29) showed that in man the ossification begins before there is a real cartilage in the precartilaginous clavicular basis, and hence with perfect justice pointed out that it was really a membrane bone.

Fawcett (*Journ. Anat. and Phys.*, vol. xlvii. pp. 225–234) has given an excellent account of the whole process of ossification, extending previous descriptions. He shows that ossification does take place in the "curious tissue, generally alluded to as a peculiar form of precartilage," before the appearance of any genuine cartilage cells, but starts from two centres, perhaps correlated with the muscle insertion, and that subsequently cartilage appears in which ossification then takes place.

These facts seem to establish the view that the cartilage in the human clavicle is really a neomorph, analogous to that which develops in the mammalian lower jaw (the reptilian dentary, a pure membrane bone) and in the mammalian pterygoid and other facial bones. The clavicle of Dicynodon differs in no respects except shape, and its inner connection with the interclavicle, from the Therian clavicle, and, like that bone, undoubtedly gave origin to the deltoid and insertion to the trapezius and cleido-mastoid muscles.

There is no doubt that the clavicle of Dicynodon is strictly homologous with that of Cynognathus, which in all its relations, and even in shape, agrees with that of the Pelycosaurs, where in some forms (Ophiacodon) its lower end is ornamented on the outer surface, and undoubtedly lay in the skin just as does the similar bone in Seymouria and the large amphibia.

We may therefore regard it as certain that the Therian clavicle is homologous with that of Stegocephalia, and contains no other elements whatsoever.

2. *Interclavicle.*

The interclavicle in the rachitomous amphibia and in Seymouria is a flat plate shown by its ornamented ventral surface to lie in the skin. From this bone, obviously of purely dermal origin, there is a complete series, passing through the Pelycosaurs, Deinocephalia, and Gorgonopsia to Cynognathus, where it is a broad flat plate with a median ridge which no doubt separated the insertions of the pectoral muscles. That this element is homologous with the interclavicle of Echidna has never been doubted; their relations to the clavicles and sternum carry conviction.

In lizards (Fürbringer, *Jena. Zeit.*, vol. xxxiv. pl. xv.) the cleido-mastoid and trapezius have an insertion on the interclavicle, caudal of the clavicle, and the muscle is continued by the interclavicular-sternal ligament to the sternum. In Sphenodon there appears to be no insertion of this muscle into the interclavicle, although the ligament is still present.

In Echidna, the superficial portion of the m. episterno-cleido-mastoideus is inserted into the anterior face of the interclavicle, and the sterno-mastoid passes over this bone to an insertion on to the ventral surface of the sternum. Both Monotremes have the power of depressing the head to an enormous extent, until the lower surface of the mandible rests on the ventral surface of the chest in Echidna. It seems very probable that these two muscles, which have an origin from contiguous parts of the skull, and run down the neck together, are really separated parts of one muscle, originally inserted on to the interclavicle, and that the more superficial part has shifted its insertion backwards as an adaptive modification to allow of this great depression of the head. If this is so, both must be derived from the interclavicular part of the cleido-mastoid of lizards, in which indeed the insertion is functionally carried back by ligaments to the sternum.

The Theria in their adult state present no definite traces of an interclavicle, but the conditions shown in my model of the 11·5-mm. Trichosurus shoulder girdle suggest that this element is really represented by the omosternum (a view already held by Gegenbaur so far as concerns insectivores). The mass of dense connective tissue representing this element is clearly marked off from all others in front, and has a definite sharply defined shape. Its relations to the inner ends of the clavicles, coracoids, and sternum are altogether those of an interclavicle, and it gives insertion to the sterno-mastoid, which, as I have tried to show above, the interclavicle originally did. Finally, the fact that ossification commences in it before

the appearance of any cartilage cells shows that it really is the representative of some membrane bone, and none except the interclavicle ever appears in this region of the Tetrapod shoulder girdle.

3. *The Homology of the Mammalian Coracoid.*

It is now generally believed on abundant evidence that the Tetrapods arose from the Rhipidistia—that is, the Osteolepid fish.

In these animals an ossification in the cartilaginous shoulder girdle usually occurs, which in good material of Rhizodopsis and Megalichthys which I have examined consists of a single small bone on each side, bearing, in the latter genus at any rate, a deep hemispherical glenoid cavity, below which it is extended towards the middle line.

In the embolomerous amphibian Pteroplax the scapulo-coracoid is a single plate-like bone of somewhat irregular shape, with a distinct scapular blade.

In the rachitomous amphibians Archegosaurus and Actinodon, there is conclusive evidence that the scapulo-coracoid is a single ossification, and no evidence has been brought forward to show that any Lower Permian rachitomous amphibian had more than one bone in each side of its cartilaginous shoulder girdle.

There are thus considerable grounds for believing that the reptiles are descended from ancestors which had only a single scapulo-coracoid element surrounding the glenoid cavity and extending into both scapular and coracoidal regions. It is possible that this condition is preserved in the Diadectids, where no specimens have shown any sutures in this region.

Seymouria is in nearly all ways the most primitive of known reptilia; the only feature which is unquestionably advanced is the loss of the cleithrum. It is remarkable that in this animal there are only two elements in the scapulo-coracoid; as there can be little doubt that some reptilian ancestor had only one, it is not improbable that when (for some quite obscure reason) the single bone was broken up in reptiles it was at first ossified from two centres, a third being subsequently added. Thus in this character Seymouria may actually be primitive.

Other groups of Cotylosaurs (Captorhinids, etc.) have clearly two coracoidal elements.

Case (1910, *Carnegie Inst. of Washington Publ.* 55, p. 157) endeavoured to show that the Poliosauridæ are the most primitive group of Pelycosaurs and may be regarded as morphological ancestors of the larger forms allied to Dimetrodon, "Theropleura" being an intermediate form. I have recently supported this view by quite new evidence drawn from the brain-case and stapedial and temporal regions which was not available

at the time of Case's discussion (*Bull. Amer. Mus. Nat. Hist.*, vol. xxxv. arts. xxxi. and xxxii. pp. 611–648, 1916).

I have shown (*Proc. Zool. Soc.*, 1914, pp. 749–786) that the Deinocephalia are the most primitive as they are the oldest known group of South

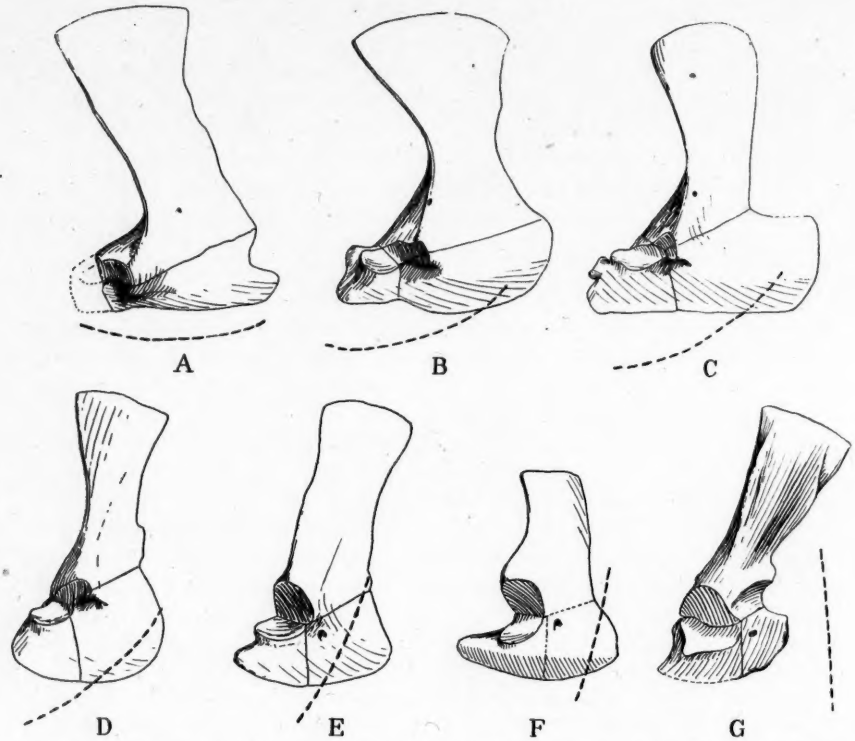

FIG. 26.—Series of Anomodont scapulo-coracoids reduced to the same size. A, Varanoops, after Williston; B, Ophiacodont, gen. nov., after Williston; C, Dimetrodon; D, "Rhophalodon"; E, Phocosaurus; F, *Scymnognathus tigriceps*, from the figure of Broom and Haughton; G, Cynognathus, from the type specimen and the original of fig. 8.

African mammal-like reptiles. Comparison of faunas suggests that the Deinocephalia from the copper-bearing sandstones of the Urals are older and more primitive than the well-known South African representatives of the order.

Finally (cf. *Proc. Zool. Soc.*, 1914, pp. 1021–1038, and *Ann. and Mag. Nat. Hist.*, ser. 8, vol. ii. pp. 65–79, 1913), there can be no reasonable

doubt that the Gorgonopsidæ are ancestral to the Cynognathidæ, being in all ways more advanced than the Deinocephalia.

If we place in correct time order, and in the sequence suggested by the known advances in structure of other parts of the skeleton, a series of drawings of the scapulo-coracoids of animals belonging to the groups referred to above, reduced to the same absolute size, we see in an extremely clear way that throughout the history of the group the anterior coracoidal element tends to be reduced in size compared with the posterior bone. In Varanoops the posterior coracoid is unossified and the anterior one enormous; in Cynognathus the anterior is very much smaller—in fact, scarcely more than half the size of the posterior. General considerations derived from a study of many similar series, which show a steady change of character in a definite direction, make it extremely probable that in still later members of the stock the anterior coracoidal element will disappear entirely.

This series of figures (which are accurate drawings made with great care) shows also that, whilst in the early forms, up to and including the Deinocephalian "Rhophalodon," the anterior coracoidal element supports part of the glenoid cavity, in all the later members the articular surface lies entirely on the scapula and posterior coracoidal element.

The evidence that the mammals arose from this group of reptiles is now so extensive and so varied in character that this hypothesis is as well supported as any phylogenetic speculation. The resemblance of the cartilaginous coracoid of the 11·5-mm. Trichosurus to the bony coracoid of Cynognathus is so close in all ways as to establish their homology; and as the one bone developed in the coracoid of the marsupial takes part in the formation of the glenoid cavity, there can be no doubt that this element, the true mammalian coracoid, is homologous with the posterior element in the Anomodont shoulder girdle; for it is inconceivable that the anterior element, which is undergoing steady reduction in this group and is finally excluded from the glenoid cavity, should suddenly reverse its evolutionary trend, functionally replacing a bone which is steadily growing larger and playing an increasing part in the glenoid cavity.

That this view is correct is indicated also by the fact that the marsupial coracoid gives origin to the coraco-brachialis and short head of the biceps, which were presumably attached to the posterior element in Anomodonts, whilst the long head of the biceps, originally attached to the anterior element, has migrated into the scapula, and the subcoracoid and supra-coracoid muscles attached to that element have totally vanished.

We are therefore justified in calling the posterior element coracoid, and the anterior precoracoid.

4. *The Homology of the "Epicoracoid" of Monotremes.*

The "epicoracoid" of Monotremes was regarded by Owen and other early workers as the homologue of the precoracoid of the early reptiles. Later authors—Parker, and at the present time Gregory (*Ann. New York Acad. Sci.*, vol. xxvi. pp. 317–383, pl. iv.)—believe it to be a neomorph homologous with the imperfect ossification or calcification which is so largely developed in the large anterior cartilaginous continuation of the coracoid of lizards. This view appears to be founded mainly on the fact that it does not articulate with the scapula as the precoracoid does in Anomodontia.

In Cynognathus (figs. 8 and 9) the small precoracoid projects very considerably in front of the scapula, and only meets that bone in a relatively short suture. The anterior hook formed by this bone in the Cynodonts is on the whole strikingly like that formed by the "epicoracoid" of Monotremes.

That the Monotremes have never lost their precoracoid, as the other mammals have done, is, I think, demonstrated by the occurrence in them of epicoraco-brachial and epicoraco-humeral muscles exactly corresponding in their attachments and relations, and, if we may use Sphenodon as a term of comparison, in their innervation to the m. subcoracoideus and m. supracoracoideus of the Anomodonts. If, then, the preservation of these muscles shows that the Monotremes never completely lost the precoracoid, it seems an unnecessary complication to refuse to see in their epicoracoid (a probably secondary enlargement of) the precoracoid. The fact that the long head of the biceps arises from the "epicoracoid" in Monotremes, instead of from the scapula, seems to afford an additional reason for regarding that bone as the precoracoid. This secondary enlargement of the precoracoid in Monotremes is due to the fact that in them the rounded head of the humerus allows of a considerable antero-posterior motion of that bone in a horizontal plane, which does not occur in Cynognathids but is a special adaptation connected with the mode of burrowing found in both Monotremes, which demands such motion, to throw the earth excavated backwards and outwards, and to enable the animals to get their hands as far or nearly as far forwards as the tip of the snout. This motion is performed largely by the epicoraco-brachial and epicoraco-humeral muscles attached to the precoracoid.

5. *Determination of the Homologous Muscles in Reptiles and Mammals.*

In the descriptive part of this paper I have examined in considerable detail the structure, possible motions, and musculature of the shoulder in many forms.

In the series of figures in fig. 26 I have indicated by a thick dotted line the direction of motion of a point connected with the distal end of the humerus. This series shows how in a perfectly regular way the direction of motion of the humerus changes from a plane parallel to the ground in Varanoops to one at right angles to it in Cynognathus.

This change of direction is dependent on the fact that the anterior part of the glenoid cavity, which at first lies very low down—in fact, nearer to the ground than the caudal end—gradually rises when traced through the three families of Pelycosaurs, the Deinocephalia, etc.

The process is as if the anterior and posterior parts of the glenoid cavity were twisted round on an axis passing through the middle of its length, the cranial end being raised and thrust backwards, the caudal end depressed and moved towards the head.

The exact resemblance between the insertions of the scapulo-humeralis anterior on the humerus of a Pelycosaur and of Sphenodon raises a strong presumption that in the Permian reptile, as in the living one, this muscle had its origin from the outer face of the scapulo-coracoid over the scapulo-precoracoid suture.

In Cynognathus (p. 27) there is conclusive evidence that this muscle occupied the whole exterior face of the scapula between the two strong flanges of that bone. This being the case, it follows that this muscle has been twisted round in the same way as the glenoid cavity, so that it no longer runs antero-posteriorly but dorso-ventrally.

This alteration of the origin of the scapulo-humeralis anterior necessarily involves a similar change of the scapulo-humeralis posterior, which, from an origin on the outer surface of the blade of the scapula in Pelycosaurs, comes in Cynognathus to have an origin on the posterior edge of the scapula.

Its insertion in both forms is on the dorsal surface of the posterior edge of the humerus below the head and in close connection with the latissimus dorsi. In Cynognathus its origin and insertion are identical with those of the teres major in both Monotremes and the 11·5-mm. Trichosurus, and I think the homology of the muscles is clear.

In Pelycosaurs (p. 16) the muscles fall into two groups: one solely concerned with the support of the animal, and with resisting rotation of the humerus; the other group, the supracoracoid and scapulo-humeralis anterior, clavicular deltoid, and the subcoracoideus, coraco-brachialis longus, and posterior part of the pectoralis, are concerned with the advance and retirement of the humerus, and the animal is driven forwards solely by them.

The subcoracoideus and supracoracoideus can have no function except

the antero-posterior motion of the humerus on a plane parallel to the ground; and when in Cynognathus this motion, if not totally impossible, at any rate becomes of very slight importance to the animal, the muscles are reduced, the precoracoid, whose main function is to give origin to them, being of correspondingly small size.

Comparison of the discussion of the mode of walking in Cynognathus (p. 29) with that of a Pelycosaur (p. 13) shows that the former is superior in all ways:—

1. The track is narrower, and hence the animal's weight is not thrown so violently from side to side.

2. The stride is longer.

3. The motions at the elbow are restricted to a single plane, and the more vertical position of the fore-arm allows of a great reduction of the flexor muscles of the fore-arm.

4. All the muscles passing from the animal's body to the arm are used at one phase or another to drive the animal forwards; in particular, the large scapulo-humeralis anterior plays a very important part in pulling the humerus back at the beginning of the stroke. Thus by these modifications Cynognathus gains a far more effective progression, and does it with a much smaller mass of muscles whose centre of gravity tends to be nearer to the body.

The Theria present a still further advance on Cynognathus. In them the humerus swings round until it lies in a plane nearly parallel to the sagittal plane of the animal, and the relatively long legs allow of the feet being placed under the centre line of the body and retained there throughout their motion, so that the body scarcely sways at all from side to side The absence of any great stress resulting from the animal's weight tending to move the fore-arm at right angles to the plane, including the axis of the humerus, and normal to the broad surface of the lower end of the humerus allows of a very great reduction of the flexor and extensor muscles, the animal's weight being largely taken by the triceps.

The existing musculature of Therians is probably not directly explicable on any mechanical theory postulating ordinary walking as the end to be obtained, because there are strong reasons for believing that all Theria, both marsupials and eutherians, have passed through an arboreal stage at an early period of their history. To the tree-living adaptations then acquired are perhaps to be attributed, amongst many other things, the round head of the humerus, the comparative slenderness of that bone, the great reduction of the coracoid, and the division of many originally single muscles into distinct parts, which occur in mammals.

The Monotremes are unique amongst living Tetrapods in that the

acromium and spine form the real anterior edge of the scapula, there being a well-defined m. supraspinatus arising from the inner surface of the bone and running down through the fossa formed by the scapula, clavicle, and precoracoid to be inserted on the greater tuberosity of the humerus in close relation to the infraspinatus.

Study of the development in man (W. H. Lewis, *Amer. Jour. of Anat.*, vol. i., 1901, pp. 145–182, pls. i.–xi.) and Trichosurus (p. 40) shows that in these types in early stages the supraspinatus arises from the inner surface of the scapula and from its anterior edge, a fact which establishes a strong presumption that the Monotreme condition is really primitive. That this view is correct is rendered almost certain by the fact that the conditions in Dicynodonts, the only reptiles with a typical supraspinatus, are identical with those in Monotremes so far as concerns these statements. The Dicynodonts are, however, different, and more primitive than the Monotremes in retaining an anterior part of the scapula, which articulates with the precoracoid and lies on the inner side of the lower part of the supraspinatus.

In Cynognathus, where I have shown (p. 28) there is no supraspinatus, the acromium lies in the same position as in Dicynodon, and that part of the scapula which articulates with the precoracoid is obviously homologous in the two genera. Now, in Cynognathus that part of the outer surface of the scapula which lies below the acromium is sharply depressed, and affords origin to a special separated part of the m. scapulo-humeralis anterior inserted on the dorsal surface of the humerus close up to the head and extending forwards to the region of the greater tuberosity. Expansion of the muscle, either in length to give increased range in action, or in thickness to increase its power, can only take place either by extending the scapula forwards, which makes its pull more horizontal, or by winding the muscle over the edge and giving it an insertion on the inner surface of the scapula, a course which gives it a more vertical action. As the mode of walking in Cynognathus calls for no increased motion of the humerus in a horizontal plane, it is evident that the latter is the modification which is most likely to ensue.

Once the detached lower portion of the scapulo-humeralis anterior has attained an origin from the inner surface of the scapula, its pull, transmitted over the edge of the scapula between the acromium and the precoracoid suture, will tend to emarginate this border, producing the notch which we actually find in Dicynodon. Further reduction of the precoracoid leads directly to the condition in Monotremes.

This account of the origin of the supraspinatus from a detached lower anterior portion of the scapulo-humeralis anterior, and of the infraspinatus

from the rest of that muscle, is consistent with their innervation in mammals and Sphenodon and their neighbouring insertion on the humerus.

In Theria the supra- and infraspinati to a large extent change their function. In Cynognathus, where their insertion is on to the dorsal surface of the humerus distal to the head, they raise that bone—a function also efficiently performed by the teres major, latissimus dorsi, and scapula deltoid.

In Theria, by the migration of their insertions on to the lateral surface of the greater tuberosity, and the throwing forwards of that region in front of the head of the bone, they become depressors of the humerus, taking over in a more simple way the function of the coraco-brachial muscles, which are hence reduced in size and somewhat altered in function, the coracoid shortening rapidly in sympathy when it no longer needs to extend far down and inwards to give origin to a muscle depressing the humerus.

The only outstanding mammalian shoulder muscle whose origin is unknown is the teres minor.

Consideration of Evidence commonly regarded as Opposed to some of the Conclusions reached above.

In the preceding discussion I have carefully refrained from discussing the views of previous authors, because it is impossible to make a long argument intelligible if it is constantly interrupted by references to other views often themselves involving knowledge of a long series of argumentative statements.

Discussion of the shoulder girdle has long ranged round the homologies of the coracoidal elements, and has in my opinion been led into most unprofitable paths by extended comparison with the Anuran shoulder girdle.

The Anura are a group of extraordinarily specialised animals of totally unknown ancestry, and why their shoulder girdle, quite unlike that of all other Tetrapods, should commonly have been taken as a primary term of comparison, as if its morphology were well understood, is obscure except for the idea that it could be made to square with Gegenbaur's view that the mammalian clavicle had a cartilaginous base and was a representative of the precoracoidal region of the cartilaginous shoulder girdle of Urodeles.

As we now know (*vide* p. 47, *antea*) that the mammalian clavicle is considerably ossified before any cartilage cells appear in its matrix, and as it can be traced by a close series of forms down to the dermal clavicles of

the Labyrinthodonts and fish, this view of Gegenbaur's and the huge literature which rests on it have become only of historical interest.

Professor G. B. Howse (*Journ. Anat. and Phys.*, vol. xxi., 1887, pp. 190–198, pl. viii.) in an important paper adopted Gegenbaur's view that the mammalian clavicle included a representative of the precoracoid, and was hence driven to the necessity of finding a new homology for the epicoracoid of Monotremes, which he showed to ossify in a suturally separated sheet of cartilage late in life.

In this paper Howse showed that in the rabbit the coracoid process contains two centres of ossification—a posterior which forms part of the glenoid cavity, and an anterior which does not enter into the articular surface but gives origin to the coraco-brachialis and biceps short head. Subsequently (in *Proc. Zool. Soc.*, 1893, pp. 585–592) he showed that these two bones occur in many orders of mammals, including man, where the glenoid epiphysis is the posterior element.

Professor Howse argued that the comparative constancy of this element shows that it is really of morphological significance, and that it corresponds to the posterior element in Monotremes, the universally occurring anterior element being the epicoracoid. It is impossible to bring conclusive evidence either for or against this view, but the evidence of muscle attachments considered on p. 52, and the total loss in Theria of those muscles whose origin is from the epicoracoid of Monotremes, is so strong as to leave no real doubt that Howse's view is incorrect, the posterior bone being a neomorph analogous to the cotyloid bone of the mammalian acetabulum.

The view adopted by Howse, that the "epicoracoid" of Monotremes is not homologous with the precoracoid of Urodeles, really rests on Gegenbaur's incorrect belief that the mammalian clavicle includes a precoracoid representative. Strictly speaking, there is no precoracoid in Urodeles, but only a cartilaginous process to which the term is by courtesy extended.

No one who compares the cartilaginous shoulder girdle of such a Urodele as Cryptobranchus with that of Deimetrodon is likely to doubt that the precoracoid of the reptile is ossified in a cartilage strictly homologous with the precoracoid process of the amphibian.

The series of forms discussed in this paper demonstrates the identity of the precoracoid of a Pelycosaur and the Monotreme epicoracoid. The name coracoid is therefore strictly applicable to the posterior element of the early reptile shoulder girdle. The Cuvierian name epicoracoid applied to the anterior element in the Monotremes is the technically correct name for the anterior element of the old reptilian shoulder girdle; but owing

to the fact that this term has been constantly applied by many anatomists to the unseparated cartilaginous extensions of the coracoids of lizards, and of the coracoidal ends of the shoulder girdles of frogs, in which true bones are never found, it seems advisable to discontinue the use of the word in its original sense to avoid grotesque confusions.

The term precoracoid is unfortunately subject to very similar drawbacks, having—in addition to its legitimate use for the anterior part of the coracoidal cartilage in Urodeles and bones which develop in a homologous region in early amphibia and reptiles—been applied by Parker, and especially Fürbringer, to a mere process of the single coracoidal element in lizards and birds—a totally incorrect and quite unnecessary use.

In this paper I have shown that many early reptiles and amphibia are characterised by a remarkable screw-shaped glenoid cavity, which restricts the humerus to a single definite motion, and through a long series of forms have traced the changes, all in the direction of greater mechanical efficiency, leading from this type to the mammalian condition. I regard it as certain that this type of glenoid cavity is the primitive form, or rather that it represents a condition through which all groups of amphibia and reptilia have passed.

In fig. 27 I have drawn of the same size two shoulder girdles of Pariasaurs from the Tapinocephalus zone and two from the later Cistecephalus zone. This series shows a rotation of the glenoid cavity, and probably, from the high position of the acromium in the later forms, of the m. scapula-humeralis anterior, exactly similar to that occurring in the mammal-like reptiles. With this change is also shown a gradual thrusting of the elbow towards the body, which in the last form, Pariasuchus, has gone to a remarkable extreme, the glenoid cavity facing very nearly backwards.

Many other groups of reptiles and amphibia show slight traces of derivation from this characteristic early form; including, for example, the living Cryptobranchus, where the strange form of the articular face of the glenoid cavity, discovered by Anthony (*Int. Cong. Med.*, 1913), receives a ready explanation by such descent, and amongst reptiles the little lizard-like Broomia with only a single coracoidal element.

In this paper I have not so far considered any one of the living reptiles or birds. These animals are remarkable in that they never have more than one coracoid bone—a fact that has been needlessly obscured (especially by Fürbringer) by the description of a mere process of this bone as precoracoid, and sometimes by the misunderstanding of the superficially calcified epicoracoid.

There is no doubt that there really is only a single coracoid in lizards,

Sphenodon, Chelonia, and crocodiles; no author, so far as I know, having ever claimed to see more than a single ossific centre.

The problem now arises, to which of the two coracoidal elements of the early reptile shoulder girdle is this bone homologous. Until a few years ago, all authors believed that the lizard coracoid was the posterior element, and was thus entitled to its name. In 1911, however, Professor S. W. Williston (*American Permian Vertebrates*) described the shoulder girdle of Seymouria and Varanosaurus, in which the posterior element, the true coracoid, is unossified, and showed that the precoracoid in these forms agrees exactly with the single coracoid of a lizard in shape, relations, and its perforation by a supracoracoid foramen. This view has been accepted by

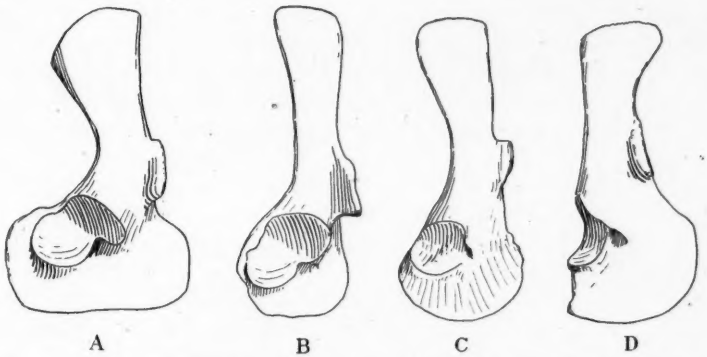

FIG. 27.—Series of Pariasaur scapulo-coracoids. A. Embrithosaurus; B, *Bradysaurus baini*, after Seeley; C, *Pariasaurus Karpinskyi*; D, Pariasuchus, after Broom.

Broom (*Anat. Anz.*, vol. xli. pp. 625–631), and seems to me to be certainly correct. Thus the single bone in lizards, etc., is the precoracoid. Williston and Broom both assume that the primitive condition is to have two coracoidal elements, and that Seymouria and Varanoops have lost the posterior. In view of the facts (1) that Seymouria is much the most primitive known reptile, (2) that Varanoops is one of the most primitive of all Pelycosaurs, (3) that the precoracoid steadily decreases in size in mammal-like reptiles whilst the coracoid grows, and (4) that the embolomerous and Lower Permian rachitomous Labyrinthodonts have only a single ossification in each side of the cartilaginous shoulder girdle, as do the Osteolepid fish,—it seems to me more probable that the true coracoid has not yet been acquired in Seymouria, Varanoops, and lizards, than that it has been lost.

The old view, that the lizard coracoid is the homologue of the posterior

element, will be supported, if anyone should think such work worth while, by arguments drawn from the Chelonia, Plesiosaurs, and birds.

In opposition to the old view of Owen, that the strong process which runs inwards from the scapula towards the middle line in tortoises is an exaggerated acromium, many authors, of whom Fürbringer is the most important, have held that this process is the precoracoid. It is extremely probable that but for comparisons with the Anura this view would never have arisen. The scapula including the process is always single, and according to W. K. Parker ("A Monograph on the Structure and Development of the Shoulder Girdle and Sternum," *Ray Soc.*, 1868, p. 141) ossifies from a single centre. The recent description by Jaekel (*Palaeontologisches Zeitschrift*, vol. i., 1914) of a shoulder girdle of a Triassic Chelonian in which the acromium is small and there is no trace of a precoracoid of any kind, removes any doubt that Owen's view was perfectly correct.

In the case of Plesiosaurs, the huge acromium which in both phylogeny and ontogeny grows forwards from the anterior edge of the scapula until it meets its fellow of the opposite side and extends back to the coracoid, has been interpreted by Fürbringer, Hulke, and Lyddeker as precoracoid, because of its resemblance to that of Chelonia. The series of growth stages of the shoulder girdle of Cryptocleidus figured by Andrews (*Ann. and Mag. Nat. Hist.*, ser. 6, vol. xv. pp. 333–346), when considered in connection with the Nothosaurian shoulder girdle, show beyond all question that the entire bone is scapula. (In a later paper I shall give a mechanical explanation of the form of an Elasmosaurid shoulder girdle, derived from an analysis of the stresses to which it is subjected.)

The only bird which really enters into consideration is Struthio, in which Parker and Fürbringer recognise, in the bar of bone which extends down to the sternum in front of and separated by a vacuity from the coracoid, a precoracoid. No evidence has been brought forward to show that this bar ossifies separately, and its interpretation as precoracoid again rests on prior conceptions. In any case, a hypothesis of skeletal homologies which requires to be bolstered up with evidence from the frogs, turtles, Plesiosaurs, and birds, and these groups alone, has little to recommend it, as the first group is obviously degenerate, the second extremely modified by the unique shell, and the last two extraordinarily specialised for very unusual habitats.

Some Considerations regarding the Origin of the Tetrapod Fore-limb from that of Fishes.

The remarkable shoulder girdle and fore-limb which is shown in this paper to provide the starting-point from which all those of mammals, reptiles, and amphibia are derived is at first sight very dissimilar to that which we should expect to be directly derived from a fish fin. In it the restriction of the humerus to a definite track and the great freedom of motion at the elbow are marked differences from the freedom at the joint between the shoulder girdle and proximal radial in fish and the slight freedom between this radial and the rest of the fin. This type of limb, however, leads to a grouping of muscles and to the restriction of the function of each group to one definite purpose, either support or progression, which probably involves a much less elaborate correlative apparatus in the nervous system than the mechanically superior condition in Cynognathus, where every muscle is used for both support and progression.

This more satisfactory arrangement is made possible in Cynognathids by the highly developed cerebellum which occurs in that group (*Ann. and Mag. Nat. Hist.*, ser. 8, vol. xii. pp. 217–228).

Any fish climbing out of water and progressing on the land depends on its fins, first for progression, which is easily obtained by moving the fin horizontally when its distal end rests on the ground, and second, in a more advanced stage, for raising its body from the ground; this last function will clearly follow the actual shuffling along.

It is evident that the original motion of punting the animal along will be carried out at the original fish fin joint between the scapula and the proximal radial; and as (*a priori*) the body of the fish is not raised, this motion will be strictly in a plane parallel to the ground. It seems probable that to this stage belongs the initiation, of course in a simple form, of the elongated screw-shaped glenoid cavity. When it becomes necessary to raise the body, the problem of correlation of muscle movements is much simplified if motion producing such effect does not take place at the same joint as that driving the animal along. The obvious way of doing it is to depress the front edge of the fin, which will be done by muscles running from the axis of the Euthenopteron-like (short archipterygoid) fins along the pinnately arranged preaxial branches. I have endeavoured to show (*Anat. Anz.*, vol. xliv. pp. 24–27, 1913) that the primitive axis of a Tetrapod limb runs through the ulna, ulnare, 4th distal carpal, and 4th digit, the radius being the proximal preaxial branch.

Depression of the anterior border of the fin of the type postulated above will develop muscles running from the first axial element along

the first branch, from the second segment along the second branch, and so on. I see in the muscles passing from the entepicondyle and ulna to the carpal region in Tetrapods the successors of these muscles, and a remarkable confirmation of this view appears in the fact that in Urodeles no muscles pass from the radius to the palmar surface of the distal part of the limb. I therefore hold that the fore-limb of Eryops is very much what we might expect to find in an animal not long removed from the fish ancestor of Tetrapods.

Summary.

In this paper typical shoulder girdles and fore-limbs of most of the families of Cotylosaurs and Anomodonts are described, the muscle insertions being indicated and the first attempt made to determine the shoulder musculature, possible movements, and methods of walking.

Examination of a series of forms of the Anomodonts arranged in correct time and morphological order shows a gradual steady change from the conditions found in Pelycosaurs, in common with most other Lower Permian Reptilia and Stegocephalia, where the articular surface of the glenoid cavity is a screw-shaped strap corresponding to a similar surface of the humerus and restricting the motion of that bone to a simple backwards and forwards motion in a plane parallel to the ground, with the middle position when the bone is at right angles to the animal's length, to those of Cynognathus, where the humerus moves in a vertical plane at an angle of about 45° with the animal's length. It is shown that this change is associated with corresponding modifications changing the action of all the muscles, and resulting in a mechanically much superior animal.

From a consideration of the same series and of the Osteolepid fish, Labyrinthodonts, and Cotylosaurs it is suggested that originally the Tetrapods had only a single ossification, the scapula, in each side of the cartilaginous shoulder girdle; that a second, the precoracoid, is then added, and finally a third, the coracoid, which steadily increases in size in comparison with the precoracoid in the mammal-like reptiles, until in Therian mammals it alone remains, the precoracoid and the muscles connected with it disappearing after becoming unnecessary.

Evidence is led to show that the "epicoracoid" of Monotremes is the Anomodont and Urodele precoracoid, and that the omosternum of Theria is the old reptilian interclavicle.

A theory, derived from the conditions in the Anomodonts, is produced to explain the origin of the mammalian supra- and infraspinatus muscles from the reptilian scapulo-humeralis anterior, and of the teres major from the scapulo-humeralis posterior.

It is suggested that the lizards split off from the other reptile stocks before they acquired the true coracoid, their coracoidal element and that of Sphenodon, Chelonia, and birds being the precoracoid.

Old views of the homologies of the elements of the shoulder girdle are then critically discussed. Finally, it is shown that shoulder girdle and fore-limb of Eryops may have arisen directly from that of fish, under the influence of intelligible forces.

In conclusion, I have to express my indebtedness to Professor A. Dendy, through whom I had the opportunity of dissecting Sphenodon, and Professor J. P. Hill, to whom I owe a specimen of Echidna.

The whole work really rests on material which I collected in Texas and South Africa, with the assistance of grants from the Percy Sladen fund.

A CASE OF ACCESSORY LUNGS ASSOCIATED WITH HERNIA THROUGH A CONGENITAL DEFECT OF THE DIAPHRAGM.

By E. A. COCKAYNE, D.M., F.R.C.P., and R. J. GLADSTONE, M.D., F.R.C.S., F.R.S.Ed., *University of London, King's College.*

THE combination of accessory lungs with congenital diaphragmatic hernia is a very rare abnormality. The association of these two congenital abnormalities, however, although rare, is not necessarily uncorrelated or fortuitous, and it appears to throw considerable light on the manner in which accessory lungs are produced.

The specimen which forms the subject of this paper was obtained from a female infant born prematurely at the eighth month. The child at the time of birth was alive and moved, but did not breathe. It weighed 5 lbs. 7 oz., and measured 18 inches in length. The "post-mortem" examination revealed a normally developed right lung, with its three lobes of average size and shape. The left lung was much smaller than normal. It consisted of an upper and a lower lobe, each of which was much but proportionally reduced in size, though otherwise they appeared normal in shape. Below the left lung (fig. 1) were two accessory lungs, which lay one above the other between the lung and the stomach. Both were completely covered by pleura, and were attached by pedicles, below the root of the left lung and between the œsophagus and the thoracic aorta. The œsophagus was considerably anterior to the attachment of the pedicles. Both accessory lungs were of a pale pink colour, and contrasted strongly with the deep red of the right and left lungs. The upper accessory lung was roughly pear-shaped, its longest diameter being 3·4 cm. The slightly flattened pedicle was about 1·75 cm. in length and 1 cm. in width. Its point of attachment just in front of the aorta was more than 2 cm. below the lower edge of the left pulmonary ligament. In the pedicle ran two arteries, arising independently from the thoracic aorta, one arising from the right side and one from its left. Two accompanying veins opened into the vena azygos major. The nerves were apparently derived from the great splanchnic.

The lower accessory lung was irregularly lobed and fan-shaped, but when *in situ* it was folded upon itself. It measured 4 cm. in length, its vertical diameter when opened out was 4·5 cm., and in thickness it varied from 0·75 to 1·2 cm. The pedicle was 1·75 cm. long and 1 cm. wide. Its

attachment to the aorta was some distance below that of the other pedicle and lay only a short distance above the level of the lower end of the œsophagus, though as in the case of the other pedicle at a considerable distance from the œsophagus and in close relation to the anterior aspect of the aorta. The pedicle contained an artery which sprang from the left side of the thoracic aorta, and a vein which entered the hemiazygos vein. A nerve entered it from the great splanchnic.

The total length of the right lung was 5·6 cm., and of the left 3·1 cm.

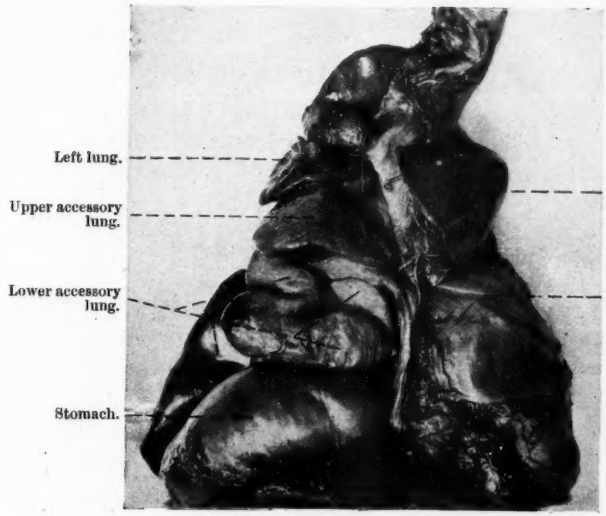

Fig. 1.—Accessory lungs of human fœtus viewed from behind.

Thus each of the accessory lungs was but slightly smaller than the right lung, and actually larger than the left lung.

Microscopically the upper accessory lung showed very numerous bronchioles lined by columnar ciliated epithelium; alveoli, lined by rather low cubical epithelium, and a thick interalveolar stroma of connective tissue containing elastic fibres. The lower accessory lung showed a division into lobules separated by connective tissue, which contained arteries surrounded by a sheath containing incompletely developed striated muscle, and lymphoid tissue which was also incompletely developed. A bronchus was present, in the wall of which lay two plates of hyaline cartilage. In the central part of each lobe were numerous bronchioles, lined by ciliated

epithelium, and in one region partly by ciliated columnar and partly by simple cubical epithelium.

A section of the left lung showed a much looser alveolar structure, with much less interalveolar tissue; and the number of bronchioles was very much smaller in comparison with the number of alveoli.

On making a comparison of the structure of the accessory lungs with that of embryonic or fœtal lung tissue, we found that their histological characters did not resemble any stage in the development of the normal lung tissue. At the stage of development when the bronchial system is as extensive as in the accessory lungs the alveoli are not yet differentiated. At a later stage when the alveoli are differentiated, the bronchiolar system is proportionately much less extensive, and the interalveolar stroma much thinner.

The Diaphragmatic Hernia.

An opening, 2.5 cm. in diameter, was present in the left side of the diaphragm. Through this opening there protruded upwards into the left pleural cavity two separate groups of organs (figs. 1 and 2):—

(*a*) Stomach.
First part of duodenum.
Part of the gastro-hepatic omentum.
A tongue-shaped lobule of the liver continuous with a peritoneal fold attached to the under surface of its left lobe, and the left triangular (or lateral) ligament.
The spleen, and an accessory spleen.
Part of the body and tail of the pancreas.

(*b*) A loop of intestine consisting of:—
Ileum.
Cæcum and appendix.
Ascending and transverse colon.
Splenic flexure and commencement of descending colon.
Mesentery and mesocolon.

The right and left kidneys with the suprarenal glands lay below the diaphragm. The opening in the diaphragm was situated in front of the left suprarenal gland. It lay behind and below the left lobe of the liver, and to the left of the œsophageal opening. It was bounded medially and behind, by the left crus of the diaphragm; while in front and to its left side it was limited by a flat muscular band (fig. 2), which was continuous medially with the left crus below the apex of the heart, while laterally it was continued backward in the left hypochondrium to the posterior

abdominal wall, where it was attached behind the left suprarenal body. The serous membrane covering the left crus of the diaphragm, when traced upwards, was continuous with the mediastinal pleura; when followed downwards, it was seen to pass on to the stomach, from the anterior surface of which it could be followed to the right, through the hernial orifice, as the anterior layer of the gastro-hepatic omentum, and to the left and downwards as the anterior layers of the gastro-lienal and gastro-colic ligaments. The membrane lining the under surface of the muscular band forming the anterior boundary of the hernial orifice was continuous medially with the left triangular ligament of the liver and the peritoneum

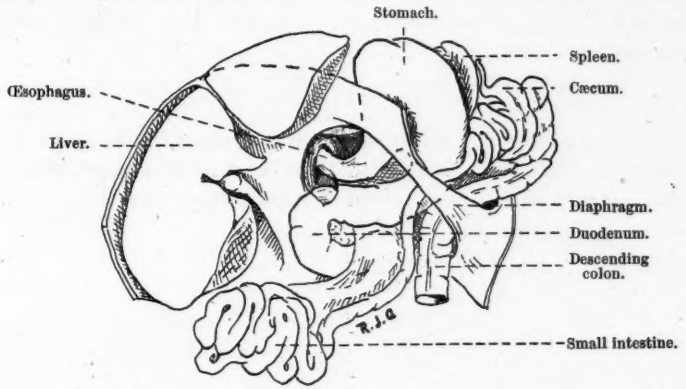

FIG. 2.—Diagram representing the position of the herniated structures, and the opening in the diaphragm.

covering the anterior wall of the abdomen. Laterally the costal pleura was continuous with the peritoneum of the left paracolic fossa. A crescentic fold, the phrenico-colic ligament, containing an accessory spleen, marked the boundary between the pleural and peritoneal cavities.

LITERATURE.

Although a considerable number of cases of accessory lungs have been reported, their occurrence must be considered as a rare event. We have been able to find in the literature of the subject 29 cases, including the one we have described, as occurring in man, and 3 in calves. Of the human, 23 are thoracic and 6 abdominal, or subdiaphragmatic. The 3 found in calves were all abdominal in position. This classification does not include tracheal and œsophageal cysts, or lung tissue contained in teratomata.

Seven of these cases, including our own, were associated with a congenital defect of the diaphragm on the left side and displacement of abdominal contents into the thoracic cavity.

Of the remaining cases in which no defect of the diaphragm was present, 19 were upon the left side and only 3 upon the right.

Cases of Accessory Lung occurring on the Right Side.

One of these was described by Dürck (7). The accessory lung was situated in the lower part of the right pleural cavity, in which it lay free, with the exception of a short round pedicle which anchored it down to the angle between the posterior chest wall and the diaphragm. The right lung appeared normal. The second, described by Simpson (28), was a case in which the accessory lung, measuring $2 \times 1\frac{1}{2}$ in. in diameter, was attached by a long pedicle to the mediastinal pleura; it lay in contact with the œsophagus, and at the level of the tenth thoracic vertebra. The right lung was small, but otherwise appeared normal. The accessory lung was situated on the diaphragm, between it and the base of the lung. The pedicle contained a large artery springing from the aorta, a vein which entered the vena azygos major, and nerves derived from both vagi. The histological structure was that of lung tissue showing cystic degeneration. The left lung was normal in all respects.

Finally, Herxheimer (11) described a right-sided specimen in which the accessory lung was situated in a totally different position. It lay above the right lung and was connected by a bronchus originating from the trachea. It was found in a male infant, who died aged three weeks.

Cases of Accessory Lung occurring on the Left Side.

The remarkable preponderance of cases of accessory lung occurring on the left side corresponds with a similar preponderance of left-sided congenital diaphragmatic hernia. Moreover, the fact that among 29 examples of accessory lungs these two conditions are associated in 7, indicates that there is a causal relationship between the two. This relation we shall discuss later, when dealing with the etiology of accessory lungs.

Of the left-sided cases four specimens possessed pedicles which connected the accessory lung to the left lung, but in none of these was there a connection of the bronchial system of the true lung, with the bronchial tubes of the accessory lung; and the accessory organs were all described as being atelectatic. In one case, however, described by Joest (14), which

was found in a calf, the mouth of an open bronchial tube was visible on the cut surface of the pedicle of the accessory lung, and according to the report of the individual who removed the specimen at the post-mortem examination, it was originally connected with the tracheal system. The air cells in the greater part of the accessory lung did not contain air; the part, however, in immediate relation with the severed bronchus contained distended air cells.

Although we have been unable to find a record of a case in the human subject in which the bronchial tubes of the accessory organ were directly continuous with the bronchial system of the normal lung, cases have been published which indicate a primary connection with the normal lung, viz.: A specimen described by Lewisohn (18), of an accessory lung in a human subject which was connected by a pedicle as thick as a lead pencil with the under surface of the lower lobe of the left lung. This pedicle contained a vessel opening into the pulmonary vein. There was, however, no connection with the bronchial system, and a second pedicle connected the accessory lung to the diaphragm, and contained an artery springing from the aorta. There was also a vein emptying into the vena azygos. This double connection of an accessory lung with the pulmonary and systemic circulations raises the question as to which of these is the primary and which is the secondary connection. A case of Vögel's (30) and another of Dubler's (6) indicate that the primary connection is the pulmonary. Both these cases were abdominal. In Dubler's case a diverticulum containing a bronchus passed upwards through the aortic opening into the left pleural cavity, where it ended blindly. In this and also in Vögel's specimen there was a deficiency in the bronchial tree of the left lung, one of its main branches being absent. These relations were regarded by Vögel as establishing the pulmonary origin of the accessory lungs in these two cases, and also of the accessory lungs having been cut off from the parent stem. His observations appear to be confirmed by a case which was reported by Hammar (10), who in reconstructing the lungs of an 11·7-mm. human embryo found that a small accessory lung, and an epithelial cyst, were separated from the upper lobe of the left lung. Corresponding with these sequestrated parts, he found a deficiency in the bronchial system of the upper lobe of the left lung. An adhesion between the separated part and the dome of the left pleura was also present behind the apex of the lung. This was probably of secondary origin, and if growth had continued, vessels would have developed within it for the nutrition of the separated part.

Etiology.

Before discussing in detail the various factors which are, or appear to be, concerned in the production of accessory lungs, it will be necessary, in the first place, to give a summary of the various theories which have been put forward by previous writers to account for their origin, and to include in this summary certain additional propositions which have occurred to us, and which we consider it necessary to discuss in conjunction with the former. In the second place, we have considered it essential, in order to give a clear conception of the merits of these different theories, to give a brief *résumé* of certain main features in the development of the lungs, and of the later stages in the development of the diaphragm. In this account we have recorded certain observations made by one of us on the relative positions of the lungs, diaphragm, and adjoining viscera in different phases of their development; also the relative positions of the pleural recess for the reception of the infracardiac lobe of the right lung, and the right pneumato-enteric recess, in rodents and carnivores; and finally, the mode of closure of the pleuro-peritoneal openings in the diaphragm. These observations are based partly upon the study of serial sections of human and other embryos, and partly on a model reconstructed by one of us (R. J. Gladstone)[1] of the lungs, diaphragm, and adjacent organs of a 16-mm. human embryo, the serial sections of which were kindly lent for the purpose by Professor J. Ernest Frazer.

This work has been undertaken, not only with the object of attempting to solve the problem of the origin of accessory lungs, but also in order to explain, if possible, the statistical correlation which exists between the formation of accessory lungs and congenital diaphragmatic hernia; and further, the greater frequency of both these conditions on the left as compared with the right side. Also because it is obvious, even from a casual inspection of cases of congenital diaphragmatic hernia, that the position of the parts forming the hernia, relative to the structures bounding the cavity into which it has protruded, cannot be explained on the assumption that a simple arrest of development has taken place at any particular phase in the development of the embryo. A further object which we have had in view has been to study the mode of closure of the pleuro-peritoneal opening of the diaphragm.

[1] Details of the latter not directly concerned in this paper will be described in a later communication.

Theories on the Origin of Accessory Lungs.

1. Accessory lungs are derived from the blastema of the pulmonary groove, a portion of which at a very early stage of development is separated from the rudiment of the lung and grows independently.

2. They originate as a separate outgrowth from the œsophageal portion of the foregut, and are not derived directly from the pulmonary bud.

3. They originate at a somewhat later stage of development as the result of adhesions taking place between the growing lung bud and the cœlomic mesothelium. That this usually but not always takes place on the left side, in the region of the pleuro-peritoneal passage, and at the time when the lung bud is in relation with the stomach, Wolffian ridge, suprarenal body, and that part of the septum transversum which covers the left lobe of the liver.

4. A portion of the growing lung bud becomes caught in an opening or recess, such as that for the "infracardiac," or "azygos lobe" of the right lung. It becomes secondarily adherent to the parietal pleura, and afterwards the adherent portion becomes separated and forms an accessory lung.

5. They arise as atavistic structures which are homologous with the pulmonary air-sacs of birds.

6. They originate as teratomatous inclusions.

The material belonging to one of us, which we have made use of for this study, consists of serial sections of the following mammalian and avian embryos and fœtuses:—

Human.

	Length in mm.	Estimated age.		Length in mm.	Estimated age.
[1]T.S.	9	4 weeks	T.S.	25	7½ weeks
T.S.	10	4½ „	T.S.	32	9 „
T.S.	11	5 „	T.S.	35	9½ „
[2]T.S.	16	6 „	T.S.	41	10 „
T.S.	22	7 „	T.S.	45	10½ „

Carnivores.

T.S. Cat, 14 mm. | T.S. Dog, 45 mm.

[1] T.S., transverse section; C.S., coronal section; L.S., longitudinal section.

[2] Specimen kindly lent by Professor J. E. Frazer, from which we have reconstructed the model represented in figs. 11 and 14, showing the diaphragm and the relations of the pleuro-peritoneal openings at this stage.

Rodents.

C.S. Mouse, 4·5 mm. (*in situ*).
T.S. „ 5 „
T.S. „ 6 „
L.S. Rabbit, 9 „
L.S. „ 12 „

C.S. Guinea-pig, 6 mm. (*in situ*).
C.S. „ 15 „ (2)
L.S. „ 15 „
T.S. „ 15 „

Chick.

T.S. 1st day (2 series).
L.S. 1st day.
L.S. 2nd day.
T.S. 38 hrs.
T.S. 48 hrs.
T.S. 3rd day.
T.S. 3 days.
T.S. 4th day.
T.S. 4 days.
T.S. 4½ days.
T.S. 5½ days.

Development of the Lungs.

The first indication of the development of the respiratory system appears in the human embryo when it has attained a length of 2·5 mm. (*Embr.*, Rob. Meyer, Normentafel No. 7). A longitudinal groove, the laryngo-tracheal sulcus, is formed in the epithelium lining the ventral wall of the pharynx; this terminates caudally in an unpaired swelling, the rudiment of the lungs. The sulcus extends from the last branchial pouches to the region of the hepatic diverticulum. The unpaired rudiment of the lungs soon becomes bilobed, and the pulmonary and tracheal parts then become separated from the gastric and œsophageal portions of the foregut by the development of two grooves, which are situated one on each side of the foregut. These project inwards and meet across the lumen of the tube, subdividing it into two parts, an anterior or tracheal and a posterior or œsophageal. Two epithelial tubes are thus formed which subsequently become separated by the interposition of surrounding mesoderm. The mesoderm which immediately surrounds the epithelial tubes and takes part in the formation of the walls of the trachea and œsophagus, afterwards becomes further differentiated by the appearance of muscular tissue in both tubes and of hyaline cartilage in the larynx, trachea, and bronchi. Leaving out of consideration the further development of the larynx, it is found that the two lobes of the bifurcated caudal extremity of the lung rudiment grow in a dorsal direction on each side of the lower end of the œsophagus into the isthmus of the cœlom, and come into relation with the septum transversum. In this situation the lung

buds pass on each side beneath a venous arch, which is formed by the union of the posterior cardinal vein with the duct of Cuvier. The concavity of this arch is occupied by a crescentic fold of the cœlomic wall. The dorsal horn of the crescent joins the posterior wall of the isthmus of the cœlom (dorsal parietal recess of His) medial to the upper end of the Wolffian ridge,[1] and lies in front of the posterior cardinal vein. The ventral horn is connected with the pericardium above, but below the level of the heart passes downwards on to that part of the septum transversum which covers the dorsal aspect of the liver. On the right side this

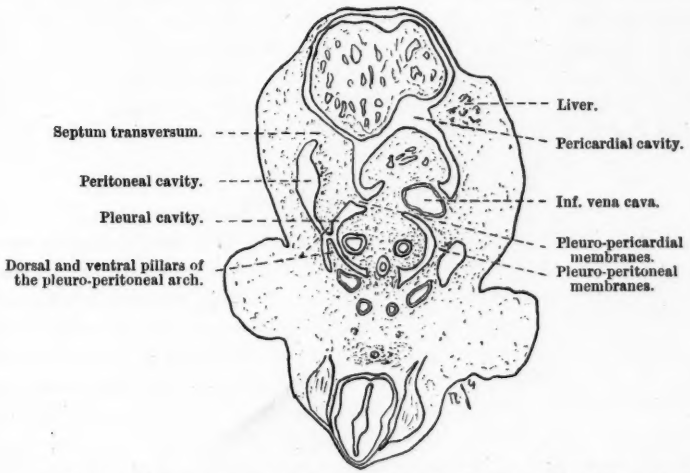

FIG. 3.—Transverse section of human embryo (9-mm.) at level of fifth cervical segment, showing the relation of the lung buds to the pleuro-peritoneal arch.

attachment is postero-lateral to the inferior vena cava (fig. 3). This crescentic fold, which in the earliest stage of development is termed by Mall (66) the "pulmonary ridge," becomes differentiated later into an upper and ventral part, the "pleuro-pericardial membrane," and a lower and dorsal part, the "pleuro-peritoneal membrane" (Uskow (80), Brachet (53)). That portion of the duct of Cuvier which becomes enclosed within the pericardium differs somewhat in its relations on the two sides, but in both it comes to lie ventral to the root of the lung, and it maintains this position in the adult. Thus we find the superior vena cava on the right, and the "ligamentum cavæ sinistræ," with the vestigial fold of

[1] On account of this relation to the Wolffian ridge, this structure has been named by Keith (65) the Wolffian fold.

Marshall, on the left side, in front of the root of the lung. Further, the terminations of the posterior cardinal veins, represented in the adult by the vena azygos and intercostal part of the superior intercostal vein, lie behind the root of the lung.

The development of the pulmonary arteries and veins is well advanced in the 10-mm. stage (His), and their relations to the main bronchi definitely fixed. The artery of the left side passes down behind the left bronchus, and on the right side in front of the eparterial bronchus but behind the hyparterial bronchus. The single pulmonary vein lies below the bifurcation of the trachea and in front of the œsophagus. It receives two tributaries on each side: the upper pair pass in front of the main or hyparterial bronchus, which thus intervenes between the pulmonary vein in front and the artery behind. The root of the lung is thus at this early stage fixed in its position, relative to the heart and main blood-vessels. The position, however, of the roots of the lungs, and of the heart, septum transversum, and liver, relative to the vertebral column, is by no means fixed. The change in the relative position of these parts has been admirably shown by Uskow (80) to be due to the forward growth of the vertebral column rather than a descent of the heart and diaphragm from the neck into the thorax. This view of the change which takes place in the relative position of the parts has also been put forward by Professor F. Wood Jones (63) in an article entitled "The Functional History of the Cœlom and the Diaphragm." The forward growth of the vertebral column is obviously associated with the early and rapid growth of the brain and spinal cord. The latter elongates both in the cephalic and caudal directions from a central region, which we may regard as a virtually fixed point, situated somewhere in the region of the umbilicus. The elongation first takes place in the arc of a circle, so that the longitudinal axis of the embryo, which in the 2·5-mm. stage is almost straight, becomes curved to such an extent when the embryo has attained a length of 7 mm., that the tip of the tail is almost in contact with the fore-brain. In an embryo of 2·1 mm. described by Mall (66), the pericardial cœlom lies anterior to the otic vesicle, and the eighth cervical myotome is behind the posterior boundary of the stalk of the umbilical vesicle. As development proceeds, the brain and spinal cord, with the nerves issuing from them, grow forward round the dorsal aspect of the heart and pericardium, carrying with them the vertebral column. Thus the bifurcation of the trachea is found opposite the fourth spinal nerve in an embryo of 6·8 mm., and to have the position shown in the following table relative to the bodies of the vertebræ, at the stages indicated under the heading, "Length of Embryo."

Length of Embyro.	Centrum of Vertebra.
9 mm.	6th cervical.
10 „	7th „
11 „	1st thoracic
16 „	2nd „
18 „	3rd „
22 „	4th „

To avoid confusion, however, we shall notwithstanding this divergence in our conception of the direction in which the growth-changes take place,

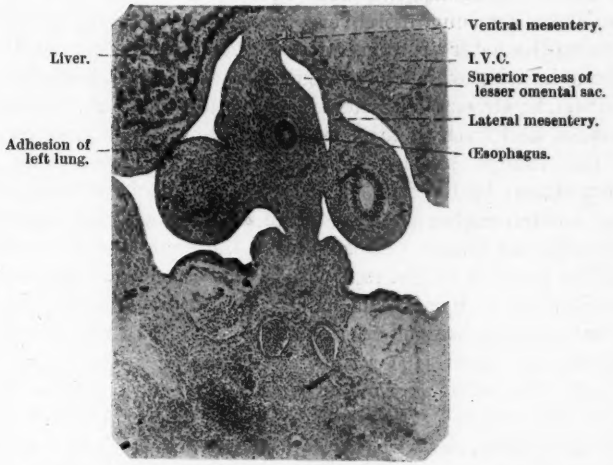

FIG. 4.—Transverse section of a 9-mm. human embryo showing adhesion of the left lung to the diaphragm.

adopt the usual description of a descent of the lungs and diaphragm relative to the vertebral column.

In embryos from about 6–10 mm. length the lungs project below the pleuro-peritoneal membrane into the peritoneal cavity, where they come into relation with abdominal organs such as the liver, stomach, and the upper end of the Wolffian ridge. At this stage the lungs may become adherent to these organs, as is shown in fig. 4, of a 9-mm. human embryo in which the left lung is adherent to the septum transversum covering the liver. The area of contact of the lungs with the liver in the 7-mm. and 11-mm. stages is well shown in two models reconstructed by Professor Peter Thompson (79). The models also show the relation of the lung buds

to the *omentum minas* (ventral mesentery) and the *plica vena cava inferior*. After this period the lungs come to lie entirely above the plane of the pleuro-peritoneal membrane and of the pleuro-peritoneal orifice. This appears to be due to the more rapid descent of the dorsal attachment of the diaphragm, relative to the vertebral column, as compared with the rate at which the lungs grow downward. After this period, therefore, should an accessory lung be formed by adhesion, and subsequent separation of the adherent portion, it would be intrathoracic rather than abdominal or subdiaphragmatic in position.

In the 10-mm. stage the main subdivisions of the bronchial system are well established, and also the subdivision of the lungs into their constituent lobes. The right lung, moreover, shows a distinct subdivision representing the "azygos" or "infracardiac" lobe of rodents and carnivores. This causes an elevation which, as has been shown by Blisnianskaja, is distinctly visible on the surface in a human embryo of 13 mm. A model of the lungs reconstructed by one of us from a embryo 16 mm. long, however, shows only a slight rounded elevation in the position of the azygos lobe; and in another model made by Blisnianskaja from a 17·5-mm. embryo, the surface of the lung has become quite smooth, and only shows the main fissures. Normally, therefore, there is at no stage of development an isolated lobule of the right lung projecting as a tongue-shaped process into a pleural recess (subpericardial sinus) behind the inferior vena cava, such as is present in the mouse or guinea-pig (figs. 5, 6, 7, 8). Moreover, when an infracardiac lobe (fig. 9) is found as an abnormality in the adult human subject, the lobe, although it may be distinctly marked off by deep fissures, does not project beyond the mediastinal surface of the lung.

In the 15-mm. stage the lungs have descended for a considerable distance. The upper extremity of the pleural cavity now corresponds in level to the neck of the first rib, and its lower to the neck of the tenth or eleventh rib. The lower pointed end of the lung reaches the ninth rib or interspace. The lungs at this stage are small compared with the size of the heart and liver, and are confined to the posterior part of the thoracic cavity. They present a posterior convex surface, and a slightly concave anterior surface; the latter is subdivided into two parts, viz.: an upper, the future mediastinal surface, which is in relation with the pericardium and phrenic nerve; and a lower, which is in contact with the septum transversum, covering the dorsal surface of the liver, and with the pleuro-peritoneal membrane. This part will become the base of the adult lung.

The apices of the lungs have now become distinct from the roots, which in earlier stages formed the highest points of the lungs. The apices at this period are on a level with the second ribs and the bifur-

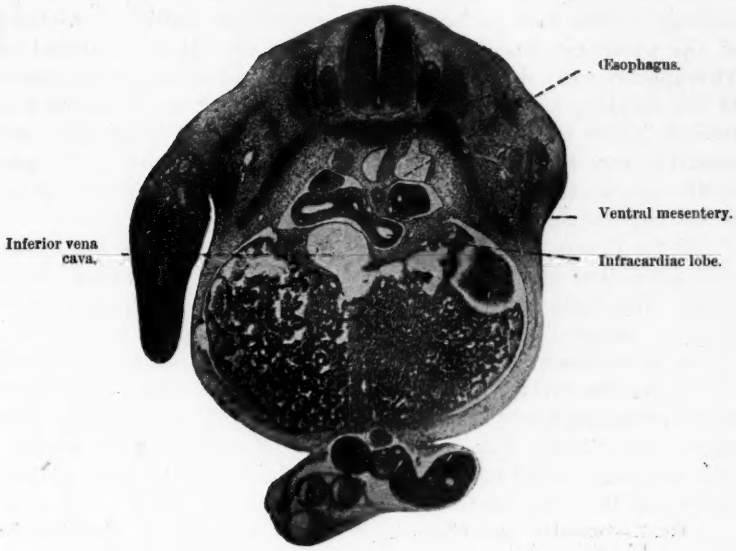

FIG. 5.—Transverse section of a mouse embryo (13 days), showing the relations of the infracardiac lobe of the right lung to the ventral mesentery, œsophagus, and the inferior vena cava.

FIG. 6.—Transverse section through a cat embryo, showing the large amount of loose mesenchyme which lies between the parietal pleura and the thoracic wall.

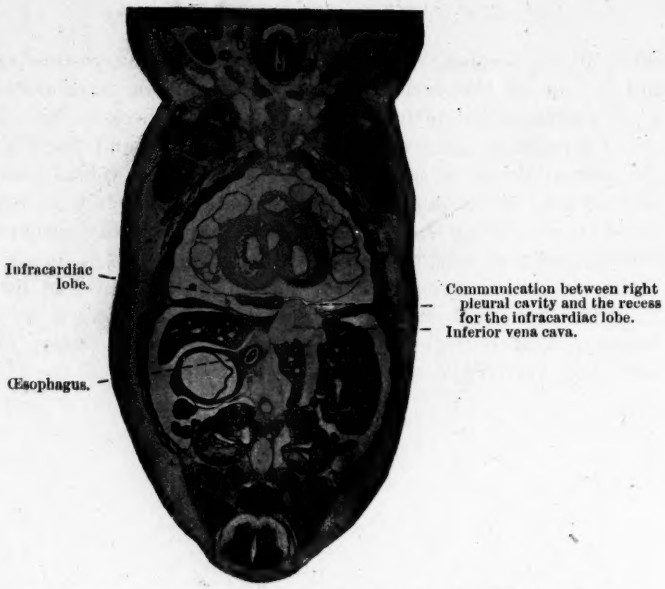
Infracardiac lobe.
Communication between right pleural cavity and the recess for the infracardiac lobe.
Inferior vena cava.
Œsophagus.

FIG. 7.—Coronal section of guinea-pig embryo, showing the relations of the infracardiac lobe of the right lung to the diaphragm, pericardium, and inferior vena cava.

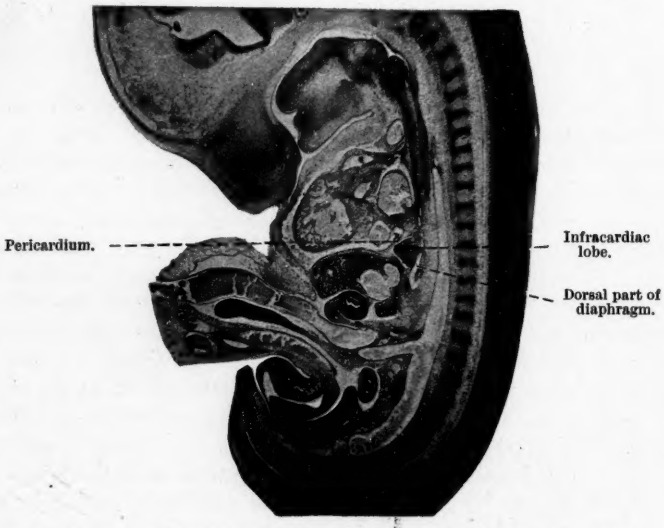

FIG. 8.—Median sagittal section of rabbit embryo (15 days), showing the relation of the infracardiac lobe to the pericardium and diaphragm.

cation of the trachea. Whether in the living embryo they extend to the full height of the cervical dome of the pleura is somewhat doubtful. The summit of the pleura corresponds to the neck of the first rib, and the difference in level of the apex of the lung and the highest point of the pleural dome, as seen in serial sections, is probably largely due to contraction. If the apices of the lungs do completely occupy the pleural dome in the living embryo, they will have already reached their permanent position relative to the thoracic wall, and it might be thought that any further growth of the lung above the level of its root would be in a downward direction from the apex. It must be remembered, however, that there is a growth in the cranial direction of the spinal cord and vertebral column relative to the root of the lung. This is

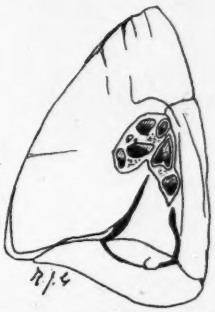

FIG. 9.—Human lung, showing "azygos" lobe.

accompanied by a shifting of the vertebral ends of the ribs and of the intercostal vessels and nerves in the same direction. There is, further, a marked elongation of the œsophagus, of the trachea, and of the pneumogastric and phrenic nerves. The heart and pericardium, with the main blood-vessels and roots of the lungs, remain relatively fixed in position, and thus appear to sink down from the neck into the thoracic cavity. There is, however, a true growth of the lung in a cranial direction above the level of its root; if this does not occur, we must assume that there is a "migration" downward of the hilum, on the mediastinal surface of the lung. Moreover, as evidence in favour of the upward growth, we may mention the occasional separation of an accessory lobe of Wrisberg, by the vena azygos major, which vessel lies at the bottom of the fissure dividing the accessory lobe from the main upper lobe of the lung. The vena azygos has obviously retained its original position relative to the root of the lung, whereas a portion of the lung has grown upward to its medial side.

In the later stages in the development of the lungs, their anterior margins grow forward in the interval between the pericardium and the thoracic wall, and appear to separate these from one another; finally, the anterior borders of the lungs meet in the middle line behind the sternum. The upper pericardial part of the anterior surface of the embryonic lung thus becomes directed medially. The lower border of the lung grows downward, this growth being accompanied by a separation of the peripheral part of the diaphragm from the deeper layer of the thoracic wall.

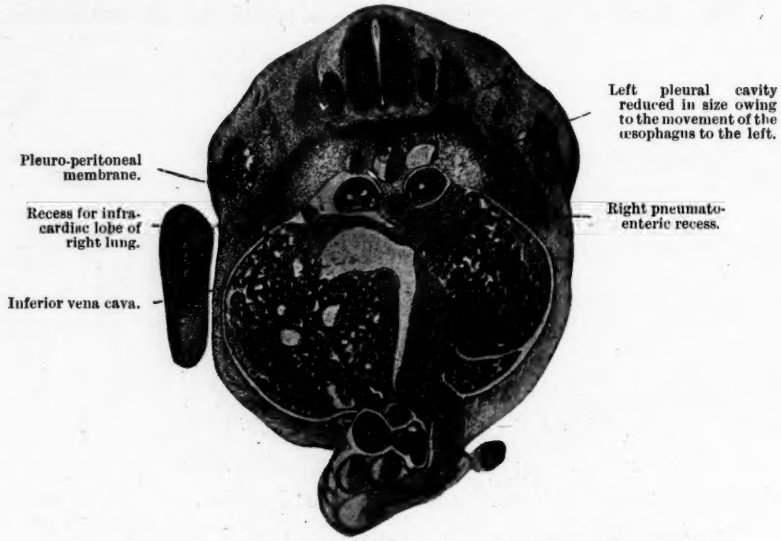
Left pleural cavity reduced in size owing to the movement of the œsophagus to the left.
Pleuro-peritoneal membrane.
Recess for infracardiac lobe of right lung.
Right pneumato-enteric recess.
Inferior vena cava.

FIG. 10.—Transverse section of a mouse embryo (13 days), showing the relation of the right pneumato-enteric recess (infracardiac bursa) to the recess for the infracardiac lobe of the right lung.

The lower diaphragmatic part of the original anterior surface of the lung now becomes the base. The extension downward of the phrenico-costal sinus of the pleura which accompanies the downward growth of the lower border of the lung corresponds in the 16-mm. stage to a plane which lies a short distance below the level of the pleuro-peritoneal opening (fig. 11).

After the opening has become closed the sinus extends further downward, and ultimately reaches a plane below the level of the neck of the last rib, which is considerably below the site formerly occupied by the foramen. The original posterior surface of the embryonic lung, which

was situated in a plane anterior to the bodies of the vertebræ, grows backwards on each side of the vertebral column. This change in position, which follows a similar change in the position of the ribs, gives rise to the rounded posterior border of the definitive lung. It is preceded by a remarkable change in the mesodermal tissue which lies between the parietal pleura and the ribs (figs. 6 and 15). This becomes extremely loose in texture, so that it resembles the mucoid tissue of the umbilical cord. At a later stage this tissue disappears and the parietal pleura then comes into contact with the ribs.

With regard to the histological features which are characteristic of

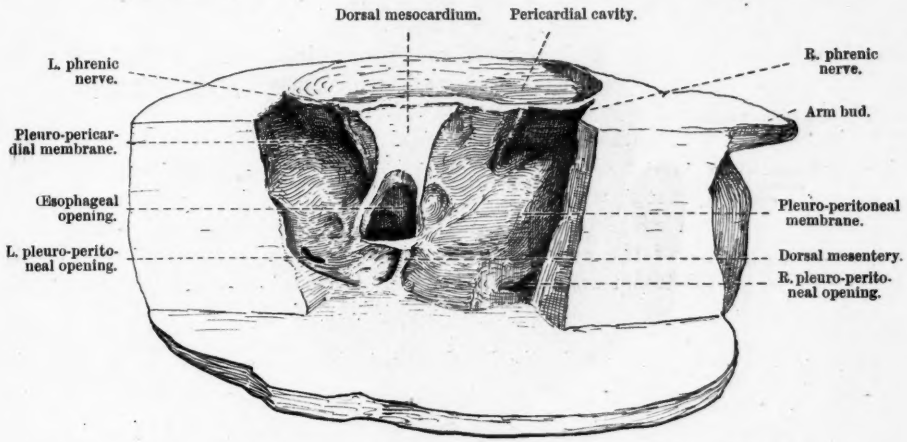

FIG. 11.—Sketch of unfinished model of the diaphragm of a 16-mm. human embryo seen from behind. Note the position of the pleuro-peritoneal openings and that the left pleural cavity is narrower and more irregular in shape than the right.

developing lungs, the most important from the standpoint of the formation of accessory lungs are, firstly, the large proportion which the connective tissue bears to the subdivisions of the bronchi in the early stages of development as compared with the condition at birth and in the adult, and secondly, the periods at which specialised histological elements such as muscle or glands make their appearance in normal development. According to Kolliker and Merkel, lobulation is present in a fœtus of 20 weeks. In the fourth month cartilaginous plates and rudimentary glands are developed in the primary bronchi, and muscular tissue is also distinguishable in the larger bronchi, which are lined by ciliated epithelium. At the sixth month the terminal bronchi are expanded into alveoli, lined by a low, flattened epithelium, and the interbronchial and interalveolar connective

tissue is much reduced. Elastic fibres, according to Linser, appear in the vessels in the third month, in the fourth month in the larger bronchi, and in the seventh month in the connective tissue—stroma.

As already stated, the structure of the accessory lungs in the case we have described does not correspond to any particular phase in the normal development of the lung, and it appears that a small portion of pulmonic tissue which has been separated from the main part, and has acquired new connections, has an extraordinary potentiality of growth. It can not only increase in size until it considerably exceeds the size of the lung from which it has originated, but it can also produce formed elements such as muscle, cartilage, and elastic tissue, which were not present at the time when it was separated from the parent tissue.

The striated muscular tissue which was present in the lower of the two accessory lungs, in the specimen we have described, may have been derived from that part of the foregut from which the upper part of the œsophagus is developed, or from the pre-muscle tissue of the septum transversum. As, however, there was no direct connection with the œsophagus, and no other histological character which in any way resembled the microscopical structure of the œsophagus, we are inclined to think that the striped muscular tissue of the accessory lung was derived from the pre-muscle tissue of the septum transversum, to which the growing lung bud had become adherent.

The Later Stages in the Development of the Diaphragm.

The next changes in development which we shall consider concern the diaphragm and the production of the hernia. In a 16-mm. embryo kindly lent by Professor J. E. Frazer the pleuro-peritoneal openings are still unclosed (figs. 12 and 13). They are, however, reduced to small, slit-like apertures with rounded margins. The opening on each side is situated lateral to the upper end of the suprarenal body, and above and medial to the superior extremity of the Wolffian ridge (fig. 14). On the right side it is in relation below with the liver. On the left it lies above an interval between the suprarenal body and the left lobe of the liver. This interval is occupied by the stomach (fig. 12). The left pleuro-peritoneal opening is therefore unprotected on its under aspect by any solid organ, whereas the right is in relation with the liver.

At this stage the intestinal loop still occupies the umbilical cœlom, and it is not normally retracted until a considerably later period, when the fœtus has attained a length of about 40 mm., whereas the pleuro-peritoneal openings close in embryos 18–19 mm. long.

The final closure of the opening appears to be due to proliferation of

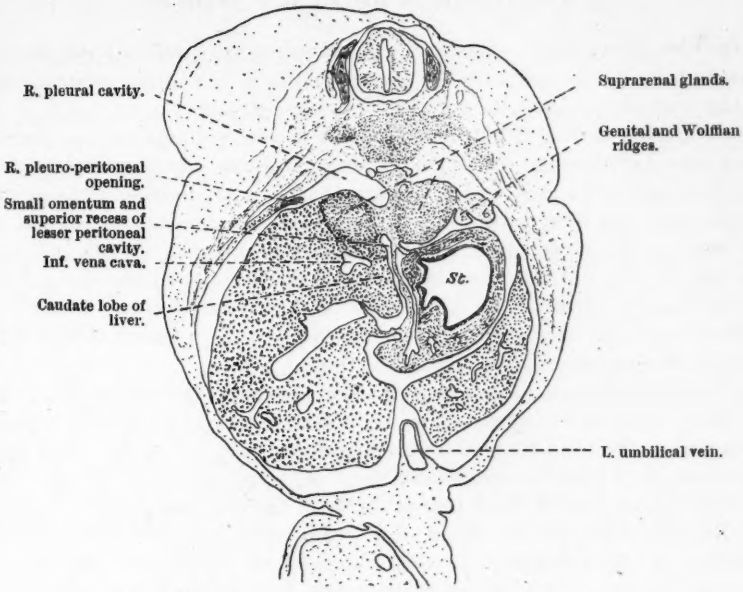

FIG. 12.—Transverse section through 16-mm. human embryo, showing the position of the R. pleuro-peritoneal opening.

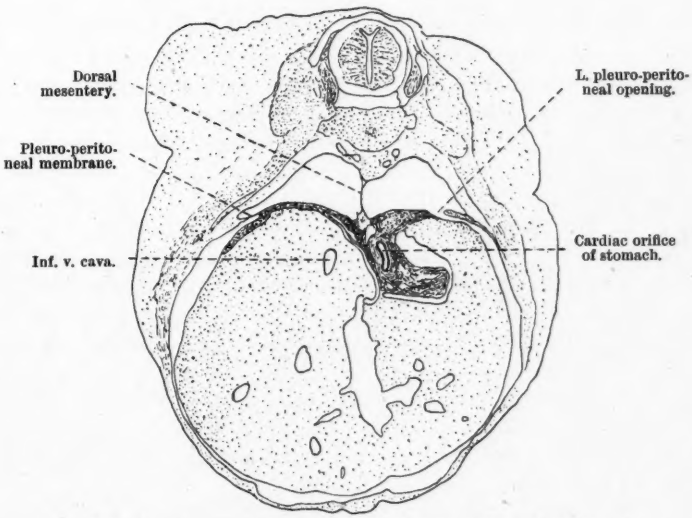

FIG. 13.—Transverse section of 16-mm. human embryo, showing the relation of the L. pleuro-peritoneal opening.

the epithelium covering its margins. The epithelium here is thickened, and stains more deeply than elsewhere. Further, the cell elements are more rounded and project irregularly from the surface of the membrane.

The exact relations of the muscle fibres of the diaphragm in the early stages of their development are difficult to determine, but it appears that the pre-muscle mass in which the phrenic nerve ends, in a 9-mm. human embryo, and which is situated just below the corresponding infra-hyoid mass, in the neck (Lewis), later becomes separated from the infra-hyoid rudiment. The latter remains in the cervical region, where it may be seen

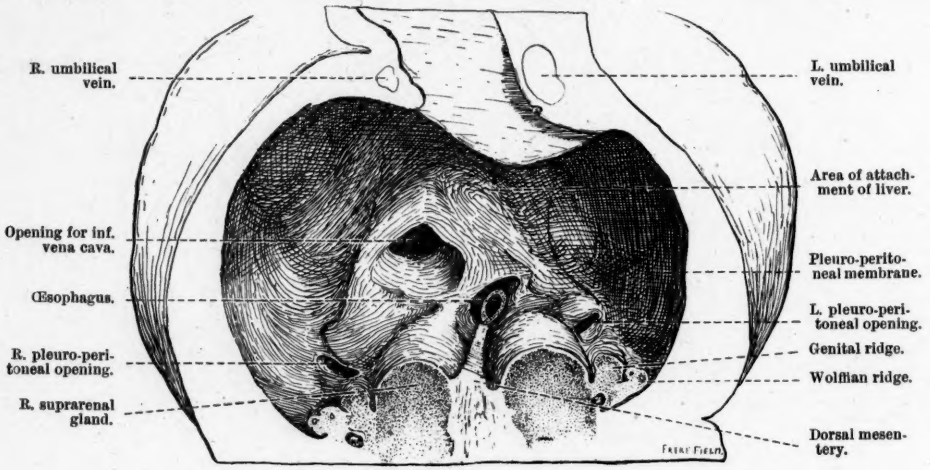

FIG. 14.—Sketch of unfinished model of diaphragm reconstructed from a 16-mm. human embryo seen from below.

passing forward in front of the upper part of the heart and pericardium (fig. 15), whereas the phrenic nerve courses downward in the body wall lateral to the anterior and common cardinal veins, and behind the subclavian vein into the pleuro-pericardial membrane. In embryos of about 15-mm. length it ends in a thickened mass of tissue (fig. 15) at the junction of the pleuro-pericardial membrane with the septum transversum, and here it divides into two principal branches, an anterior and posterior, which apparently correspond to the definitive branches in the adult, and to the costal and vertebral segments of the muscle. In embryos of from 20 mm. onward, when muscular tissue is distinctly recognisable, the muscle fibres of the costal segment appear to be continuous laterally with the m. transversus abdominis, whereas the fibres of the vertebral segment

course downward in the dorsal mesogastrium to form the crura of the diaphragm.

The triangular gap between the costal and vertebral attachments of the muscle is completely closed by the pleuro-peritoneal membrane. The pleuro-peritoneal opening, as previously stated, appears to be closed by

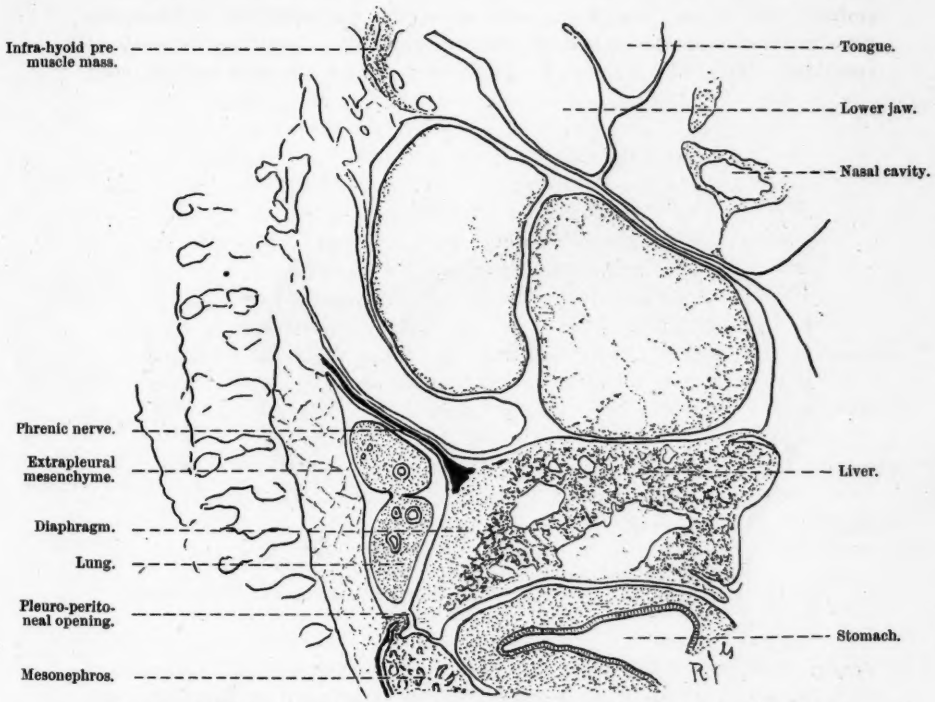

FIG. 15.—Sagittal section of rabbit embryo (16 days) passing through the pleuro-peritoneal opening and showing the termination of the phrenic nerve in the pre-muscle tissue of the diaphragm.

proliferation of the cœlomic epithelium bounding the aperture. It seems probable, therefore, that the muscle fibres grow downward in the pleuro-peritoneal membrane separating pleura from peritoneum, and also into the dorsal mesentery; and further, that the closure of the pleuro-peritoneal opening is independent of the triangular gap, the hiatus diaphragmaticus, which is left between the adjacent edges of the muscular sheets.

Having considered the more important developmental conditions which

must influence the production of accessory lungs, and of congenital diaphragmatic hernia, we shall now briefly discuss the different theories, already mentioned, which have been advanced to account for their occurrence.

1. One of the most attractive of these hypotheses is, that accessory lungs are derived from the pulmonary blastema of the original laryngo-tracheal groove, a portion of which at a very early stage of development has become separated from the parent tissue and has taken on an independent growth.

We think it quite possible that this mode of origin may account for the formation of accessory lungs in certain atypical situations, but it is difficult on this hypothesis to offer any explanation for the preponderance of cases of accessory lung on the left side as compared with the right, or to account for the high proportional frequency with which accessory lungs are associated with a defective development of the diaphragm on the left side and congenital diaphragmatic hernia.

2. The same objection applies to the hypothesis of Eppinger and Schauenstein, who regard them as independent pulmonary organs, arising from an additional outgrowth from the foregut, in the region of the "dorsal parietal recess" and "septum transversum." Bert and Fischer (3) support these authors by pointing out that cysts occur in the wall of the œsophagus, some lined by both ciliated and squamous epithelium, some by ciliated epithelium alone, and others lined by ciliated epithelium which have plates of cartilage in their walls. They regard these as transitional to true accessory lungs. It is, however, more probable that such cysts arise from the pulmonary groove, from which they become separated owing to the rapid elongation of the foregut which takes place in the formation of the œsophagus. Their position in connection with the lower end of the gullet and in the vicinity of the cardiac orifice of the stomach is thus readily explained. The occurrence of cysts lined by ciliated epithelium in relation with the trachea, and sometimes in communication with its lumen, is an additional point in favour of this view of their origin. Œsophageal cysts also are quite as often situated to the right or in the middle line as to the left of the œsophagus.

3. The theory that accessory lungs are formed by an adhesion taking place between the growing lung bud and the cœlomic epithelium, and that a portion of the adherent lung tissue subsequently becomes separated off from the main part and takes on an independent growth has much in its favour. It appears to afford an explanation of the greater frequency of accessory lungs on the left side as compared with the right, and also of the association of these with a defect in the development of the left side

of the diaphragm, and congenital hernia of abdominal organs through this defect. As already mentioned, we have ourselves observed such an adhesion present in two human embryos, one 9 mm. (fig. 4) and the other 10 mm. longest diameter (C.R.M.). The adhesion was in the same situation in both, namely on the left side, between the lung bud and the septum transversum, covering the dorsal aspect of the liver. Both specimens were macerated and probably pathological. Adhesions of the lung to the parietal pleura may, however, be observed in perfectly healthy embryos, *e.g.* we have noticed an extensive adhesion of the lower and medial portion of the left lung to the parietal pleura which lines the niche between the œsophagus and its dorsal mesentery in a 16-day rabbit embryo. The tissues in this specimen appear to be quite healthy and are well preserved. Whether such adherence of the lung to the adjoining tissues in this situation is primary and due to delay in the separation of the lung bud from the mesodermal tissue of the mesentery, or is a secondary condition, does not affect the argument that accessory lungs may arise from such an adherent portion of the lung becoming separated off from the main organ so as to form an independent structure. Secondary adhesions, moreover, normally take place in the same situation as in the human embryos mentioned above, but on both sides in the chick embryo, and are permanent. Their occasional and probably temporary occurrence in the human embryo may therefore possibly be atavistic rather than pathological. In the chick embryo these adhesions are associated with the development of the pneumato-enteric recesses. According to Lillie (93), "the accessory mesentery grows" forward on each side in the interval between the "lateral mesocardium" and the ventral mesentery and adheres to the septum transversum. Later the entodermal lung sacs grow into the accessory mesenteries, and thus lie lateral to the pneumato-enteric recesses. On the left side the accessory mesentery ceases opposite the lower extremity of the lung, but on the right side it is continued back by the mesentery of the inferior vena cava as far as the middle of the stomach, where it is attached to the septum transversum at the superior lateral angle of the liver.

The very much greater frequency of accessory lungs on the left, as compared with the right side, points to there being some mechanical condition which is present on the left side but not upon the right, and we would suggest that there is a tendency for the lower end of the developing lung bud to adhere to the structures in relation with the pleuro-peritoneal passage at the time when the septum transversum and liver are descending from the upper to the lower part of the thoracic portion of the trunk.

At this stage a rapid change in the relative position of the parts takes place on the left side. The lower end of the left lung, which at first is in

close relation with that part of the foregut which will become the fundus of the stomach, and with the left lobe of the liver, becomes separated from these by the pleuro-peritoneal membrane, which is developed in continuity with the lower part of the pulmonary ridge. The lung thus comes to lie above and dorsal to the membrane and the plane of the pleuro-peritoneal orifice. We believe that it is at this critical phase of development, involving the above-mentioned change in the relative positions of the adjacent organs, that the lung is apt to become adherent to one or other of the neighbouring structures.

A factor which we would suggest may be responsible for the adhesion of the lung bud to the cœlomic epithelium taking place more frequently on the left side than on the right is that the normal movement of the stomach to the left, which commences in embryos about 4·5 cm. in length, carries the lower end of the œsophagus, with its dorsal and ventral mesenteries, and the lung buds also to the left (see figs. 4, 6, 10), thus reducing the size of the left pleural passage and widening that of the right. The left pleural space is thus distinctly narrower than the right, and in serial sections of embryos, in which as a result of "fixation" the lung buds are seen to have retracted away from the thoracic wall, the lung appears to more completely fill the pleural cavity on the left side than on the right. At a later stage in development the width of the left pleural cavity is still further reduced by the projection of the heart and pericardium more to the left than the right side.

Another factor which would favour adhesion on the left side is that the mesodermal lobes formed round the second dorsal bronchus and the terminal part of the stem bronchus of the left lung, lie in especially close relation to the lower end of the œsophagus, and occupy a niche formed between its dorsal mesentery and the thoracic wall. This is the position in which accessory lungs are commonly found, as for instance the case which we have described. This relation of the above-mentioned lobes to the œsophagus is well shown in a reconstruction by Hammar (90) of an 11·8-mm. human embryo.

If such an adhesion should fail to break down, a small portion of the lung tissue might become separated and remain in relation with the liver, stomach, diaphragm, or dorsal mesogastrium. The separated part, cut off from the bronchial system and pulmonary circulation, would draw its blood-supply from the vessels of the part to which it has become adherent; thus we find accessory lungs with arteries derived from the left phrenic artery, cœliac axis, or thoracic aorta, and the veins passing into the portal system, hemiazygos, and azygos veins. The position of the pedicles, and the vessels contained therein, varies according to the site of the original attachment,

and may be subdiaphragmatic (intra-abdominal) or intrathoracic. The specimen described by Lewisohn (18), and previously mentioned, in which an accessory lung was connected with the left lung by one pedicle, and with the thoracic wall by a second pedicle, appears to us to afford very strong evidence in favour of the origin of accessory lungs by adhesion to the cœlomic epithelium lining the pleural passage or covering an adjacent organ such as the liver or stomach; and the theory is further supported by the cases described by Dubler (6) and Vögel (30), and that of Hammar, in which an accessory lung adherent to the cervical pleura was associated with a defect, corresponding in position to it, in the bronchial system of the adjacent portion of the lung.

4. A modification of the last-mentioned theory is that which attributes the origin of accessory lungs to a portion of the lung becoming caught in an opening or recess such as that for the "infracardiac" or "azygos" lobe of the right lung. The part thus caught, being subsequently separated from the main portion, contracts adhesions to the wall of the sac. The position of the pedicle, however, in the cases which have been recorded is usually posterior to the œsophagus, whereas the azygos lobe passes to the left, behind the inferior vena cava but anterior to the œsophagus (figs. 5 and 6). Further, although in the human subject an "azygos lobe" is represented in the bronchial system of the embryo, and may occur as an abnormality in the form of a separate lobe in the adult, there appears to be no separate recess in the pleural cavity for its reception. The upper end of the right pneumato-enteric recess, which is described by Broman in human and other mammalian embryos as being cut off to form the infracardiac bursa, is an independent structure quite distinct from the recess (sinus subpericardiacus) which contains the infracardiac lobe of the right lung (fig. 10).

We consider, therefore, that though the azygos lobe may be cut off in the way suggested in those animals in which it normally exists, this view of the origin of accessory lungs cannot be entertained as far as the human subject is concerned.

We think it quite possible, however, that an accessory *lobe* such as Wrisberg's could be completely separated off from the parent stem and thus form an accessory *lung*.

5. The theory that accessory lungs are homologous with the lower pulmonary air-sacs of birds is one which deserves careful consideration, for it is into the "accessory mesenteries" previously mentioned that the entodermal air-sacs of the avian embryo extend, and if the adhesions of the lungs described above as occurring in the human embryo are regarded as atavistic in nature, the accessory lungs arising as a result of these

adhesions might be regarded as homologous with the air-sacs. We are inclined, however, to regard the condition in the human subject as pathological rather than atavistic, more especially on account of the frequent association of accessory lungs with other defects, which may be attributed to faulty nutrition of the embryo.

6. The last hypothesis which we shall consider is, that accessory lungs originate as teratomatous inclusions. Although lung tissue has been found along with other tissues or organs in the teratomata, or mixed tumours, these nearly always occur in the form of a definite tumour, surrounded by a cutaneous or fibrous capsule, and though they have been found in the mediastinum of the thorax (inclusio mediastinalis), or within the abdomen in the region of the umbilicus (inclusio abdominalis), they are not found free in the pleural or peritoneal cavities. Thus, whether they are regarded as parasitic in nature, or as aberrations in the development of a single fœtus, they differ essentially in character and situation from the typical accessory lungs, and we consider that they belong to a totally different category.

Congenital Diaphragmatic Hernia.

Passing now to the anatomy and mode of development of the congenital diaphragmatic hernia, so much has already been written on this subject that it will only be necessary for us to draw attention to certain points which so far as we know have not been previously considered. It is commonly stated that a congenital diaphragmatic hernia is not a true hernia, but rather the persistence of an early developmental phase, in which the pleural and peritoneal cavities are continuous with one another, and the stomach is intrathoracic in position. Now, in those cases in which the stomach and colon are both present in the hernia, although it is not usually precisely stated, there must be two loops forming the hernia: (1) consisting of the stomach and sometimes the first part of the duodenum, with the body of the pancreas and spleen, and (2) the terminal part of the small intestine, cæcum, appendix, and the colon as far as the splenic flexure. The descending and terminal parts of the duodenum and the head of the pancreas are intra-abdominal and approximately normal in position. Further, the œsophageal opening of the diaphragm, which is situated in that part of the diaphragm which is developed from the mesentery of the foregut, is complete and separate from the hernial aperture. It is, moreover, at its normal level. The œsophagus, therefore, does not run a direct course to the highest part of the stomach, as it would do if the condition was a mere persistence of the early embryonic

condition. The œsophagus passes down usually to the level of the ninth thoracic vertebra, it then, after having pierced the diaphragm, becomes continuous with the proximal limb of the "stomach loop," running a recurrent course upwards from the cardiac orifice to the fundus. It is

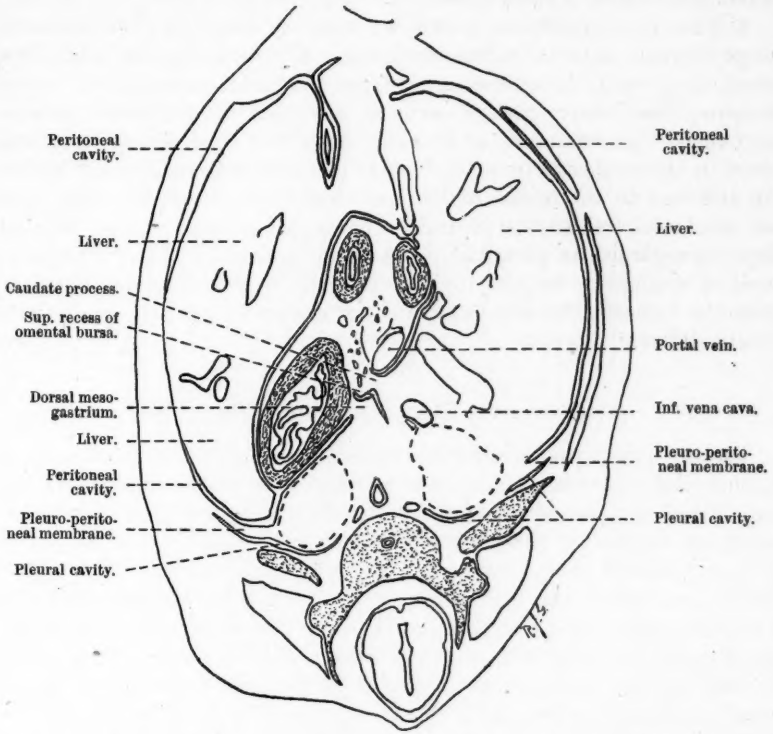

FIG. 16.—Transverse section of a human embryo (22 mm.), showing the relation of the pleuro-peritoneal membranes to the suprarenal bodies and liver. The outlines of the suprarenal glands are indicated by interrupted lines.

obvious, therefore, that the "stomach loop," with the body and tail of the pancreas and spleen, must have been displaced upwards from the abdominal cavity into the thoracic. Secondly, the "intestino-colic loop" is developed from a part of the primitive canal, which in the early developmental stages lies outside the body of the embryo altogether in the "umbilical cœlom," and retains this position until long after the time when the pleuro-peritoneal openings in the diaphragm are normally closed. They therefore must

also be displaced upwards through the hernial aperture, and form a true hernia into the thoracic cavity.

With regard to the nature of the hernial aperture and the period at which the hernia takes place, allusion has already been made to the unprotected area in the region of the left pleuro-peritoneal opening between the left suprarenal body and the left lobe of the liver. This area, after the opening has become closed (18–20-mm. stage) (fig. 16), is covered merely by the pleuro-peritoneal membrane. Later, muscular fibres are developed in the membrane which separate pleura from peritoneum. If the normal closure of the opening should be delayed, the muscle fibres if traced downwards will be found to diverge on each side of the aperture, so that the costal fibres will bound it laterally, the vertebral or crural fibres medially. In most cases of congenital diaphragmatic hernia it is probable, however, that there is not only a delay in the closure of the opening, but a defect in the development of the diaphragm. In extreme cases this appears to be primary, but in others it might be explained by the pressure of the herniated viscera. It is possible that the cause of the delay in the closure of the pleuro-peritoneal opening in cases in which accessory lungs are associated with a hernia may be the adhesion of the lung to the liver, stomach, or cœlomic wall. It is, however, obvious that in the vast majority of cases of congenital diaphragmatic hernia the cause of the delay in closure of the opening, or imperfect development of the diaphragm, must be attributed to a defective nutrition, probably due to disease of the chorion or placenta, since the condition is frequently associated with other defects in development.

Those cases in which the herniated organs are covered by a membrane are probably to be explained by a failure in the development of the muscle fibres; the thin pleuro-peritoneal membrane is thus unable to resist the pressure of the viscera and becomes stretched out over them. It is quite possible, however, that the membrane instead of yielding would be ruptured, in which case a secondary opening would be formed in the diaphragm, at the margins of which the pleura and peritoneum would become continuous, thus resembling a persistent pleuro-peritoneal passage or isthmus of the cœlom.

Summary.

The principal points which we have discussed in the preceding pages and which we wish to emphasise are the following:—

1. Accessory lungs are derived from the embryonic tissue of the "pulmonary groove," or of the "lung buds."

2. A portion of the embryonic pulmonary tissue, after having become

adherent to a neighbouring part or organ, from which it draws its blood-supply secondarily, may be separated from the parent tissue and grow independently.

3. We believe that the small size of the left pleural cavity, and the close relation of the mesodermal lobes of the left lung to the lower end of the œsophagus (see p. 88), would favour adhesion of the lung taking place on this side, and this may account for the greater frequency of accessory lungs on the left as compared with the right side.

4. It is probable that accessory lungs do not ordinarily originate as a secondary and independent outgrowth from the œsophageal portion of the foregut.

5. The adhesion of the lung bud to the septum transversum covering the liver, or to the wall of the pleuro-peritoneal passage in typical left-sided cases of accessory lung, may interfere with the normal retraction of the lung bud from the abdomen into the thorax, and cause a persistence of the pleuro-peritoneal opening. We are thus able to explain the occasional intra-abdominal position of accessory lungs, and the association of accessory lungs with left-sided congenital diaphragmatic hernia.

6. The closure of the pleuro-peritoneal openings is normally due to proliferation of the mesothelium covering the edges of the openings.

7. This closure of the pleuro-peritoneal openings is independent of the development of the muscular fibres of the diaphragm.

8. At the time when the pleuro-peritoneal openings normally become closed, the intestinal loop is situated within the umbilical cœlom, and it appears probable that congenital diaphragmatic hernia is due to the persistence of the opening, and takes place at the time, or after the return of the intestines into the abdomen.

9. The hernia usually consists of two loops:

(1) The stomach, with the spleen and part of the pancreas.
(2) The terminal part of the small intestine, and the colon as far as the splenic flexure.

The duodenum and head of the pancreas are nearly always intra-abdominal.

10. A congenital diaphragmatic hernia is a true hernia, both in those cases in which the contents of the hernia are covered with a serous membrane and those in which they lie free in the pleural cavity.

11. A congenital diaphragmatic hernia cannot be regarded as a simple arrest in development, or persistence of any particular stage in the formation of the embryo.

In conclusion we wish to express our gratitude to Professor J. E.

Frazer for the loan of his serial sections of a 16-mm. human embryo from which the model of the diaphragm figs. 11 and 14 has been reconstructed, and to Professor Barclay Smith for kindly revising the manuscript, and the kind interest which he has taken in the work.

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FORM AND FUNCTION OF TEETH: A THEORY OF "MAXIMUM SHEAR."

By D. MACKINTOSH SHAW, *Royal Dental Hospital, London.*

THIS concept, "maximum shear," has been applied to explain in a more precise manner than has hitherto been done the functional meaning of many specific features in the shapes of teeth. It offers also, in the case of man's dentitions, an explanation of the chewing mechanism that fits all the observed dynamical conditions and actual results. If it be granted that teeth were evolved mainly for their utility in manipulating food, then a close and persistent study of dental mechanism from the "machine and tool-action" point of view is a very rational and promising method of interpreting the physiological meaning and value of any morphological feature or detail in teeth. It would seem, *a priori*, that the definiteness and constancy that characterise each specific feature in the form of a tooth might well be directly related to a like definiteness and constancy in function or functions. If a morphological feature remains, in a clearly recognised sense, fixed and distinctive throughout that particular species, the functional requirement that evoked and preserved it is admitted to be, in several *obvious* instances, similarly fixed and distinct. But the same relationship most probably exists in the less obvious instances, and possibly in all, or nearly all instances, if only we could discover and verify the relationship.

What here follows is an attempt to explain some of the results of my endeavours in this direction during the past twelve years. Attention for the present is confined to man's teeth, where the opportunity for inquiry and investigation is much more favourable than we would hope for in other animal dentitions.

In the dentition of perhaps every species of animal the form and mechanism of the teeth are influenced—one might almost say determined—by two conditions that are fundamental: (1) the nature of the food; (2) the degree of its reduction. In regard to the first, we know something of the nature of man's food, although unfortunately very little is known with certainty as to the nature of his "staple" foodstuffs during the period in which the main features of the normal present-day dentition were evolved and established. Regarding the second, the degree of reduction of food,

it is well ascertained that man's teeth are adapted to (that is to say, they can and do) comminute hard and tough food to a fine degree. Such distinctive characters in the teeth as hardness and sharpness must correspond to qualities of hardness, toughness and the like, in the food.

It appears, then, that in investigating man's dental mechanism the problem is mainly concerned with the behaviour of hard and tough material when subjected to certain stresses. There is perhaps no subject to which a greater amount of close scientific study and experiment has been devoted than the behaviour of hard and tough material under various stresses. An immense body of knowledge has been built up by engineers and mathematicians and applied to useful purposes, but, so far as I am aware, neither the knowledge gained nor the methods of investigation have been at all seriously applied to the study of dental mechanisms. True it is that the engineer, the physicist, and the mathematician worked mainly at problems relating to such hard materials as metal, wood, etc.; but they were and are prepared to use the same methods as far as possible in dealing with *any* material or structure that might come before them for inquiry, and no odontologist will suggest that a new kind of physics or mechanics is called for in the study of dental mechanism.

The same principles and methods will apply; although a distinct and somewhat peculiar difficulty arises from the fact that the engineers' inquiry into strains and stresses is mainly directed towards *preventing* the breakdown of material or structures, while our particular object is to find out how Nature went about to *facilitate* the breakdown of material with economy of effort.

Material is strained and may rupture or break under the action of one or more of *three principal stresses*: (1) compression; (2) tension; (3) shear. In a given case rupture may be produced as a response to *one only* of these three principal stresses, or two or the three kinds of stress may be so combined and intermingled that it is difficult to say whether a particular one predominates. More often failure takes place as the result of combined stresses, one of them playing a dominant part in the rupture.

A point on which it should be worth while to fix attention is this:— hard and tough material is more easily (requiring less effort) broken up by a shearing stress than by either a compressive or tensile stress. This is true for many metals and alloys, and for many other materials is so well recognised that the estimated "safe limit of stress" is given as considerably lower for shear than for tension or compression. The tests upon which these results were based were of course only applied to materials employed for constructional purposes. No such tests have been applied

to foodstuffs. But, relatively to metals, among the constructional materials *wood* may be regarded as approaching in some degree more towards the range of the moderate hardness and toughness found in foodstuffs. For two woods, oak and pine, the following values have been given for the breaking stress in lbs. per square inch:—

	Tensile.	Compressive.	Shearing.
Wood, oak . . .	15,000	10,000	2300
,, pine . .	12,000	6,000	650

It does not seem needful at this stage to present further evidence that, as we pass under review the action of stresses on materials possessing those qualities of hardness and toughness that lie between the extremes of metal on the one hand and fibrous foodstuffs on the other, there is found a marked and increasing effectiveness in the power of shearing as compared with tensile or compressive stresses.

Further, in any device for the break-up or reduction of material by shearing stresses, by a very simple adjustment a time factor can be introduced by which the resistance at each instant is lessened, with a consequent reduction in the magnitude or intensity of the force required. A familiar example is a pair of scissors, where the edges of the blades are so inclined to one another that the material is attacked and severed gradually, or bit by bit, and not instantaneously at every place, as would occur if the edges were parallel and coincided. It is not usually practicable to secure this particular advantage (in economy of effort) when tensile or compressive stresses are used.

Returning now to the natural chewing mechanism, it is an obvious and familiar fact that man's incisors are adapted for shearing. But in written references to the functions of the cheek teeth—whether made by odontologists, zoologists, or evolutionists—there seems to be a fixed belief, either implied or stated positively, that the cheek teeth act mainly by "crushing" or "grinding." There is a certain handiness (as well as vagueness) about these terms, "crushing" and "grinding," that makes them quite allowable in popular descriptions of teeth: unfortunately the same attributes have helped to perpetuate their use in scientific writings. In drawing attention to the fact that man's cheek teeth normally act mainly by shearing and not by crushing stresses, I would urge that the distinction is far from being a merely verbal or academic one.

My hypothesis of "maximum shear" may now be stated as follows:—
The teeth of man, alike in regard to many of their specific morphological

features, the manner of interaction between the opposing rows, and the precise character of the jaw movements that are habitual and effective, are all normally adapted and used to secure in effect the dominant condition that the shearing stresses—not the compressive stresses—are at a maximum.

The conditions that are here more or less indispensable for effective shear are: (1) a certain amount of "overlap" arranged for between the opposed shearing edges; (2) a certain degree of sharpness in the shearing edges.

Now both of these prime conditions, although usually accepted as specially and distinctively characterising the anterior teeth only, are found on examination to hold also—and in at least equally effective degree—for the cheek teeth. The amount of overlap (distance between the shearing edges when the teeth are in occlusion) may be somewhat greater in the anterior than in the posterior teeth; but that makes no difference in a close shear, the effective action of which ceases the instant that an opposed pair of shearing edges have just passed one another.

Then as to the sharpness, I find that the sharpest edges are not to be found on the incisors, but on the "cusped" or posterior teeth. It should be borne in mind that it is *normal unworn teeth* that are at present under consideration.

Examination and experimental tests dismiss any possible doubt that the *statical* conditions for efficient shearing—the form and relationship of "tool" blades, edges, and surfaces—are present and no less marked in the posterior or cusped teeth than in the incisors. And turning to the dynamical and kinematical conditions, we find that they are at least quite as favourable for efficient shearing in the cheek teeth as in the incisors. In strict fact these conditions are by one remarkable adaptation made *more* favourable for the cheek teeth, inasmuch as in the general mechanism of the "machine" there is a sliding and *guiding* contact between the canines that ensures for all the cheek teeth the precise alignment of the shearing edges that is required for efficient shear: the edges are thus also prevented from "clashing," or being needlessly deteriorated. I have observed and verified this "fine adjustment" in many sound normal dentitions, and, what is indeed remarkable, have found it also working almost to perfection in some hundreds of dentitions that were far from normal in arrangement.

During mastication, the outstanding functional effect of direct *protrusion* of the mandible is to bring the lower incisors into shearing relationship with the upper incisors; so likewise the outstanding functional effect of *lateral deflection* of the mandible is to bring the shearing edges of the

lower cheek teeth into precise alignment with the edges of the upper ones. (Diagram fig. 1, *a*, *b*, and *c*.)

THE DIRECTION of the shearing thrust between any opposed pair of teeth will be in and along the general plane in which the overlapping and coincident surfaces of the shearing blades lie. The *inclination* of those surfaces (that come into sliding contact and determine the direction of the thrust) varies with the individual or group type in the series, being somewhat vertical on the incisors and becoming progressively more horizontally inclined towards the end-member of the molar group. With advancing age and wear those surfaces or planes become more flattened or horizontal, and the shearing edges are gradually shifted outward. And it is a well-observed fact that as the cusps become worn and flattened, the character and direction of the jaw movements become altered; the lateral

FIG. 1.—Diagram showing direction of effective normal thrust in (*a*) incisors, (*b*) 1st premolars, and (*c*) molars.

deflection of the mandible becomes more marked, and the direction of the thrust more horizontal (fig. 3). The "maximum shear" hypothesis affords a clear explanation of the alteration in the character of the jaw movements in advancing age, wherein the worn and deteriorated machine endeavours, by a more and more laterally-directed thrust, to close up the failing shear and maintain the optimum shear available.

The shearing edges thus far spoken of are all on the *external* blades of the tooth row, where they lie in a smooth and practically continuous curve from one 3rd molar to the other. What about the internal row of cusps? it may be asked. It can be demonstrated that the presence of the internal row of cusps does not interfere with or prevent the shearing action of the external cusps. What then are the functions of the internal or lingual row of cusps?

To answer that question with any degree of preciseness it will be convenient to consider first that pair of opposed lingual cusps that come next to the anterior single-bladed teeth—the lingual cusps of the 1st premolars. Let us imagine that a piece of food (of a kind that requires

hard and sharp teeth to operate on effectively) has been bitten or sheared off by the incisors or anteriors. We may permit ourselves the assumption that the morsel is passed on to the premolars for further reduction. Let the diagram (fig. 2) represent a pair of opposed 1st premolars in an observed functional relationship, with a portion of the food morsel in the position indicated. The lingual cusp of the 1st *lower* premolar is so short

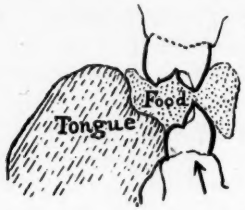

FIG. 2.—Showing function of lingual cusp during chewing stroke.

and small that—without "prejudice" to any theory of its function—it may for the moment be disregarded and attention concentrated on the bold lingual cusp of the upper premolar.

What is the upper lingual cusp actually *doing*? The accepted notion that lingual cusps were evolved to act as "crushers" is not so firmly established by proofs—or indeed so supported by any published evidence—

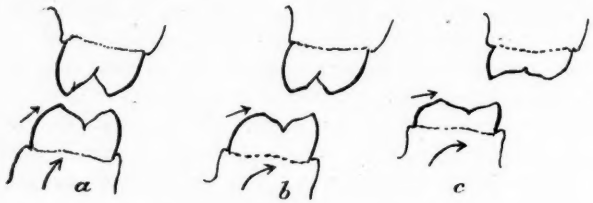

FIG. 3.—*a*, unworn; *b*, worn; *c*, more worn.

that we must refrain from making a fresh examination and inquiry. The upper lingual cusp is doing very little in the way of crushing; in point of fact it is doing even less crushing than might seem to be represented in the diagram, inasmuch as the two teeth do not, of course, come into occlusion with their morsal surfaces directly opposite, but with one rather in front of the other. A good deal of observation and experiment has satisfied me that this prominent cusp does something more important and necessary than a little doubtful or adventitious crushing; it *holds* (and helps the

tongue to hold) *the food fragment in proper position for effective shearing* by the precisely-aligned external blades.

In any shearing mechanism there must be *some* provision, either made or existing, for holding in proper position the material to be operated on. The smaller the fragment (up to a certain limit) the more elaborated or refined must be the devices required for holding it in position for further reduction—as in the molar teeth. There is firm ground for believing that a close study of this paramount requirement for food-holding devices or adaptations will prove of real value in the more rational interpretation of many of the varied cusp forms and cusp arrangements in different kinds of animal dentitions.

Returning to the masticating mechanism of man's premolars, my proposition that the external cusps are adapted mainly for shearing and the internal cusps mainly for food-holding will, it can be shown, bear well a more searching examination. The differences in form that distinguish the

FIG. 4.

outer from the inner cusps require examination in detail. Fig. 4 shows the morsal or occlusal aspect of the left upper premolars. It will be observed that the cutting edges of each buccal cusp lie almost entirely in a plane, the continuous line of the cutting edge being bent in that plane only at the cusp point. On the other hand, the cutting edges of each lingual cusp do not lie in a plane, but are crescentic and curved outwards from the cusp point. Now in both cases those are exactly the special modifications that would be of prime utility in the functions I have referred them to—the "straight," sharp buccal blade for shearing, and the curved (pointed, but more rounded) lingual blade for food-holding; more strictly—in the latter case—to *help the tongue* in food-holding, the lingual cusp being smaller and very smoothly rounded off away from the tongue, and the concavity of the crescentic cutting-edge being *turned outward* to hold the food against the inwardly-directed shearing thrust.

That the tongue by itself is a very inefficient instrument for holding *small* food fragments in position can be attested by anyone who has had the misfortune to lose all his cheek teeth. Then the work done—by the anterior teeth only—is tedious, and performed in a conscious and niggling manner; the free, rhythmical activity of normal function is conspicuously

absent. The tongue, helped by the lips, etc., can hold the larger fragments in position without risk of wounding itself; for finer reduction the assistance of an inner row of special "holders" is required.

On the molar cusps *true* crushing takes place also, but the effective so-called "crushing" and "grinding" which actually disintegrates the food is in reality—and even with much-worn teeth—mainly a shearing action.

To the food-holding interpretation of man's lingual cusps it may be objected that in many animal dentitions (selenodont, etc.) the *buccal* cusps are crescentic, and also have the concavity of the crescent turned outward. That objection might be valid and might even throw light on the functional meaning of man's cusp-forms if only something definite were known of the functional meaning of the (apparently) like features in those animal dentitions. But no definite interpretation of those specific features has yet been put forward, and the vague and general notion of a "crushing" function has so far proved to be almost completely unproductive in the field of comparative odontology. In this line of inquiry comparative work will continue to be somewhat barren in results until we search out in each type or species the two prime factors already mentioned. (1) The physical nature of the food: size, hardness and toughness, surface texture (roughness or smoothness, dry or slippery, etc.); distinct and more-or-less fixed differences in configuration, such as grasses, that are large in one dimension only—length; leaves that may be large in two dimensions—length and breadth; and fruits, seeds, roots, animal tissues, etc., that may be relatively very large *or* very small in all three dimensions. (2) The degree of reduction or comminution that has been effected when the food leaves the mouth.

Assuming that, in regard to these primary factors, adequate or the best procurable information had been gained, one would then be in a fair position to examine the general structure and mechanism of the dental apparatus, and ascertain the particular functions of its various parts. In even the simplest kind of tool there is invariably *more than one* (often three or more) requirement of construction and material found to be essential to its utility; *e.g.* a lancet must have hardness, sharpness of edge, and thinness of blade. And in a machine or contrivance of moderate complexity we can usually, after examining it at work, pick out and correctly assign to separate parts of it distinct and separate functions.

By way of summarising in some kind of related order some results of investigation on the mechanism of mastication in man the following table is presented:—

MAN'S DENTITION AND MASTICATING MECHANISM.

Relation between Nature of Work done and the Form and Function of Interacting Tissues.

1. Physical nature of food:—Hard, with some toughness; average or general size — moderate in all three dimensions.	(*a*) Blade edges of optimum sharpness, so opposed and moved as to break up food chiefly by shearing stresses. (*b*) Characteristics of surface shape adapted to protect gum tissue from injury by hard fragments during the shearing thrust. (*c*) Tongue-shielding adaptations, the "umbicle." Lingual cusp-edges retreating from lingual side. (*d*) Conditions or devices that are effective in *conserving* the optimum sharpness of cusp-edges:—the *guiding* function of opposed canines and anteriors; *deep* grooves formed by the convergence of *convex* walls.
2. Degree of its reduction:—Finely comminuted.	(*a*) Freely movable soft tissues or organs that replace and hold the food in position between the tooth rows: tongue, cheeks, lips. (*b*) Lingual cusps that *hold food in right position* during shearing stroke. (*c*) Order and arrangement of blades and cusps adapted for normal reduction of food to be progressively increased from incisors to molars. (*d*) Morphological features (general and special) so interacting as to allow of "chip clearance," and prevent the impacting and interdental wedging of food particles or morsels.

Most of the function interpretations summarised in the above table have been noted and described in some detail in previous papers (*Dental Record*, Aug. 1909, Sept. 1912, and Aug. 1914; *Nature*, July 23, 1914; and a paper presented at the International Dental Congress, 1914, Section of Anatomy and Physiology). It is not implied that some or any of these interpretations apply exclusively or uniquely to man; no more is here predicated than that certain distinctive features, relationships, movements, etc., were observed to be very effectively associated with certain useful results, and

that after prolonged search *no other or different* kind of associated utility could be observed or—in some cases—even conjectured. This is at least as high a degree of probability as exists in the numberless cases where adaptation to a particular function has been posited of an organ or part and accepted as a settled fact.

Statements made upon the functional meaning of the tooth-forms of even familiar animals are often based upon guesses and conjectures which could only be tested and verified, if at all, by prolonged and tedious research, so far unattempted. And in the controversies that turn upon the evolution of mammalian teeth, eminent zoologists, when discussing the origin and gradual progress in the phylogeny of a new or changing morphological feature in particular teeth, do not hesitate to support the argument by saying that the modification arose and persisted because of its utility in this or that more or less vaguely specified way. In the case of man's teeth, the new results summarised in the above table can be definitely verified or rejected by an investigation in which there should be no insurmountable difficulties. As the physical factors are almost entirely mechanical and relate to dynamics rather than to statics, a fair knowledge of and interest in the precise working action of tools and simple machines would be specially useful, if one may say so.

The findings tabulated under 1 (*a*), (*c*), and 2 (*d*) are interesting from the anatomical point of view; 1 (*b*), 2 (*b*), and (*c*) should be of some value to the morphologist; and the last three, considered together, offer a solution to the baffling problem of how to trace, in the *lower steps or minute beginnings*, any definite utilities by which an evolving cuspule might be supposed to climb into prominence and an obvious crushing or other function. In particular, the way in which a scarcely discernible but quite effective gum-shielding feature may become modified and enlarged, so as to take part in food-holding and other utilities, can be clearly followed out in the existing variations among normal human teeth. But adequate description of these, and a clear presentation of the related facts observed, would require another paper.

THE EARLIEST STAGES OF DEVELOPMENT OF THE BLOOD-VESSELS AND OF THE HEART IN FERRET EMBRYOS.[1]

By CHUNG-CHING WANG, M.D., Ch.B. (Edin.), *Acting Lecturer and Demonstrator in Anatomy, University College, London; late Carnegie Research Fellow in Embryology, and Assistant in the Department of Anatomy, Edinburgh University.*

INTRODUCTION.

BEFORE the details of the reconstructions which were made are given and the conclusions to which they tend are discussed, it seems advisable to state briefly the main results of the observations which have previously been made by other investigators regarding the formation of the intra-embryonic vessels and blood-cells, and the earliest stages of development of the heart in mammals generally. It is to be noted that the phenomena observed are, of necessity, intimately associated with the early stages of development of the pleuro-pericardial cavity, and are closely connected with the mode of formation of the pre-umbilical portion of the body of the embryo.

To facilitate references to be made hereafter in this communication, the ferret embryos are classified into stages. Thus in Stage I. the description deals principally with the blood-cells and vascular endothelium; in Stage II. the account relates chiefly to the first appearance of the heart rudiment as a single transverse vascular channel situated caudo-ventral to the pleuro-pericardial cavity; in Stage III. it is shown how the single heart tube is converted into two lateral heart tubes; in Stage IV. the statement refers mainly to the conditions of the two endothelial tubes and their relationships to the muscular wall of the heart; and in Stage V. the site of fusion of the two heart rudiments to form an unpaired heart tube is indicated.

As far as the technique and the histological conditions of the ferret embryos, to be immediately described, are concerned, the description given

[1] An abstract from a thesis for the degree of M.D., for which a gold medal was awarded by the University of Edinburgh.

in Stage IV. may be applied equally well to all the other specimens selected for the purpose of this investigation. The only differences to be found in this respect are chiefly in the matter of staining and in a few other minor points, such as, whether the embryo was detached or not from the uterus before being sectioned.

Blood-Vessels and Blood-Cells.

It may be mentioned at once that the question of the origin of the vascular rudiment is one of the most obscure in the realms of comparative embryology. Even the lowest vertebrates, which present the greatest simplicity in their structures and whose development is most easily understood, have failed to throw satisfactory light on this question.

There is a great diversity of opinion regarding the germ layer from which the vascular endothelium and blood-cells arise. In the literature it may be found that certain competent investigators have in each vertebrate class claimed the vascular endothelium and blood-cells to be derived from entoderm, while other workers of equal authority have found the vessels and blood corpuscles to arise from the mesoderm. It is to be noted, however, that in no case has an author stated that the blood-cells and vascular endothelium are derived from different germ layers.

Ziegler ('87) expresses the view that "the system of blood-vessels and that of the lymphatic vessels are produced in their first fundaments from remnants of the primary body cavity (blastocœl), which at the general distribution of the formative tissue (mesoderm) remain behind as vessels, lacunæ, or interstices, and are closed by that tissue and incorporated in it." This author therefore agrees with Bütschli ('82) that in all metazoa the blood vascular system has its origin from the blastocœl. On the other hand, Felix ('97) inclines to the belief that the circulatory system is, from a developmental point of view, closely related with the cœlom.

In reptiles, Strahl ('83), in birds, Kölliker ('84), in Selachians, Ziegler ('92), and in mammals, Kölliker ('84), all claim that the first vessel rudiments are found in the mesoderm and not between the mesoderm and entoderm. The current view which is held by a great number of investigators is that in embryos of the higher vertebrates, the first vascular rudiments which can be identified as the forerunners of the blood-vessels and blood-cells, appear, at first, in the form of localised cell cords lying upon the yolk-sac between the mesodermic tissue and the entoderm. His ('00) gives the name of "angioblast" to these cell cords.

Upon the question as to whether the angioblast is to be looked upon as a derivative of the mesoderm, or as an offshoot from the entoderm, opinions again diverge. In support of the mesodermic origin, the names

of Maximow ('09), Weidenreich ('10), Evans ('12), Rückert and Mollier ('06) are of prominence, while the advocates of the entodermic theory are to be found in the persons of Kölliker ('82), Robinson ('92), Keibel ('88), and Van der Stricht ('99). Miss Parker ('15), in her recent investigation into the development of the heart in Marsupials, admits the possibility of the entodermal origin of the endothelium. In Fundulus, Stockard ('15) finds that vascular endothelium does arise *in situ* in many parts of the embryonic body in which blood-cell rudiments are not present, and that independent blood islands are found on the yolk-sac.

The persistent claims that vascular endothelium has the power to change into various types of blood corpuscles have been disproved by the recent experimental work of Stockard ('15). After considerable study and careful observations, Stockard observed nothing that would indicate that the vascular endothelial cells possess the power to change into the blood-cell type, nor could he find any evidence to indicate that cells having once assumed even the earliest blood-cell type are capable of metamorphosis to form endothelial cells. He firmly believes that, in Fundulus at least, endothelium is incapable of giving rise to any type of blood-cell.

Whatever its origin, the angioblast, according to current views, is, in the majority of amniota, chick for example, found lying between the mesoderm and entoderm in the form of cell cords in the area vasculosa immediately surrounding the embryonic shield. It is believed that the peripheral part of each angioblastic strand soon resolves itself into an uninterrupted network of endothelium, and the central part into clusters of blood-cells. The endothelial cells which enclose the blood-cells continue to divide and produce vascular sprouts which appear, at first, as solid cords but later become hollow (Hertwig ('92), Minot ('12)).

Around the periphery of the area vasculosa, in the majority of animals, the vitelline plexus resolves itself into a broad circular vessel—the sinus terminalis, which is continuous round the margin of the area except at the cranial end where it terminates on each side in a vessel which enters the embryo. The vascularisation of the splanchnic layer of the mesoderm gradually extends through the extra-embryonic region of the zygote until it covers the whole extra-embryonic region, where it forms an intermediate layer between the entoderm and mesoderm.

Some of the larger channels of the area vasculosa, even in the early stage of its formation, converge to form a single vessel on each side, which enters the embryonic body through the splanchnopleure and ultimately joins the venous end of the heart rudiments when they are developed. These are the two vessels previously mentioned as connected with the cranial end of the sinus terminalis, and are known as the omphalo-mesenteric (vitelline)

veins. It is believed that other channels of the area vasculosa on each side grow towards the median plane of the embryo, and as they approach the region of the notochord their extremities fuse to form a longitudinal vessel which is the dorsal aorta of that side. The dorsal aorta ultimately unites with the arterial end of the heart. In this way the vitelline circulation of the embryo is completed and plays an important role in all vertebrates in supplying the growing embryo with nutritive materials from the yolk-sac, which is comparatively large.

In reptiles and birds, a second circulation, as it were, develops in connection with the allantois, and persists during incubation; in mammals the allantois is incorporated with the placenta which establishes the communication between the embryo and the mother, and the vessels which correspond to the allantoic vessels in reptiles and birds become associated with the placental circulation (*vide infra*).

Consideration has been confined so far mainly to the part played by vessels which in origin are extra-embryonic. The next question to be considered is whether the early blood-vessels in the body of the embryo itself are formed by an ingrowth of the vitelline plexus which is, by origin, composed of extra-embryonic blood-vessels, or whether, on the other hand, the intra-embryonic vascular system, or at least a part of it, arises *in situ* from the germ layers of the body. The problem is difficult, and it is not surprising that various conflicting views have been formulated regarding the precise mode of origin of the intra-embryonic blood-vessels. Thus, the names of Hertwig ('92) and His ('00) have been identified with the idea that the early blood-vessels in the body of the embryo itself are formed by a budding or ingrowth of the endothelial wall of the vessels from the extra-embryonic vascular area, and the name of Sobotta ('02) is associated with the belief that there is an outgrowth of the vessels from the body of the embryo to the wall of the yolk-sac. Rückert and Mollier ('06), on the other hand, maintain that the embryonic vascular stems, or at least a part of them, arise *in situ* from the mesoderm of the embryo. Other investigators, basing their opinion on the results of a series of experiments on growing chick embryos, adhere to the conviction that, even after the destruction of the yolk-sac vessels of one side, the heart, the aorta, and the other vessels are found to develop on both sides in the embryo.

On the other hand, Vialleton ('92), His ('00), and Evans ('09), who have investigated the intra-embryonic blood-vessels in birds, and to whom we are indebted for a comprehensive knowledge of the formation of the caudal portion of the dorsal aorta, come to the conclusion that the greater part of the dorsal aorta in the bird is formed from the medial margin of the

vitelline plexus which has grown into the embryo in the manner already referred to. Türstig ('84) also has noticed the frequent early connection of the primitive dorsal aorta with the vitelline plexus in mammals.

With regard to the development of the cranial portion of the aorta, on the other hand, various opposing views are held; thus, His ('00) attributes it to the result of a further growth of the same extra-embryonic vitelline plexus which forms the caudal part of the aorta, but which is reduced to a capillary chain growing headwards, eventually turning ventrally over the blind end of the fore-gut and fusing with the cranial portion of the heart tube. Lewis ('04) and Bremer ('12) both arrive at a somewhat similar conclusion, namely, that in the rabbit embryo, the dorsal aorta, the aortic arch, the conus arteriosus, and the lateral heart are all parts of an original network of angioblastic cords derived from the extra-embryonic plexus of blood-vessels. On the other hand, Mollier ('06) believes that the notion of His ('75) and Vialleton ('92) is not nearly so probable as that the individual intra-embryonic vessel cells arise *in loco* and thus form the vascular nets.

Recently the local origin of vascular endothelium received additional support from the experimental results recorded by Miller and M'Whorter ('14) on the origin of blood-vessels in the chick embryo. Such a view is further strengthened by the still more recent experimental evidence presented by Reagan ('15), which shows the origin *in loco* of vessels in isolated parts of chick embryos, and by Stockard ('15), which claims that in Teleost embryos there can be no doubt that the heart endothelium and aortæ arise *in situ* within the embryo.

It is to be noted that all these experiments just quoted confirm the earlier results of Hahn ('09) on the origin of vessels in the chick, and that the formation of intra-embryonic blood-vessels is much more extensive and important than has formerly been supposed.

Though the development of blood-cells lies without the scope of the present communication, a few remarks may be made regarding the close relationship of these cells to the vascular endothelium. Nearly all investigators on this subject assert that blood-cells and vascular endothelium arise from either the mesoderm or entoderm. In reviewing the literature on this point no definite statement has been found which might suggest that blood-cells and endothelium develop from different germ layers. The possibility of these structures having an independent and separate origin cannot, however, be overlooked, as will be seen later.

Maximow ('09) believes that the endothelial cells and blood-cells are closely related, and arise from a common stem cell in the blood island, and may continue to arise from such a cell during later development. Stockard

('15), on the other hand, states "that vascular endothelium forms in perfectly normal fashion within the heart and head regions of embryos without circulating blood, but in no case in early or late stages was the endothelial lining of the aorta or other vessels capable of giving rise to any type of corpuscles. Yet the power to form blood corpuscles was abundantly present in the same embryos as shown by the huge numbers of blood-cells within the blood-forming regions—the intermediate cell mass and yolk islands."

Maximow ('09) states further that the intra-vascular primitive blood-cells are not only increased by mitosis but are added to also by the proliferation of the same kind of cells from the fixed endothelial cell of the primitive vessels. The assumption is based on the fact that clusters of blood-cells are often seen adherent to the endothelial wall of the blood-vessels. Maximow thinks that these clusters of cells may arise by the proliferation of the endothelium. Minot ('12), however, disagrees with Maximow, because he finds that there is no continuity of the protoplasm of the cells either in the rabbit or in man; also, because mitosis of the endothelium in the neighbourhood of the clusters is almost invariably wanting; and, finally, because the endothelial nuclei are differentiated, while the nuclei of the cells of the clusters are not differentiated. Minot regards the cells composing the clusters as solely primary wandering cells, Stockard ('15) concludes that endothelial lining is utterly incapable of giving rise to any form of blood-cell.

As in mammals, before referred to, so in man, in connection with the vascularisation of the yolk-sac, or, according to Fetzer ('10), even at a period before any vascular rudiment on the yolk-sac proper can be distinguished, there develop, in the belly-stalk and chorion of the embryo, highly characteristic strands of spindle cells, which repeatedly exhibit the nature of having the appearance of a double row of nuclei and of possessing a distinct lumen. This has been observed by Graf Spee ('96) in the embryo von Herff of 37 mm. The strands of spindle cells have been claimed to form endothelial cells eventually.

In young human embryos, without any vessels or blood islands on the yolk-sac, Jung ('07) and Herzog ('09) have called attention to the aggregation of cells, sometimes arranged round a lumen, situated at the periphery of the mesoderm of the yolk-sac and belly-stalk in the neighbourhood of the extra-embryonic area. In slightly older specimens with recognisable yolk-sac vessels, irregular spaces in the mesoderm, some lined with endothelium, some without any definite lining, have been observed by many authors, and recently Grosser ('13) and Debeyre ('12) have independently described, beside the irregular spaces, true blood islands in the belly-stalk

near the allantois. In human embryo 1·17 mm. described by Frassi ('08) there is an abundance of well-formed vascular rudiments on the ventral surface of the yolk-sac, and Frassi states that with little or no difficulty vessels can be detected also in the belly-stalk and chorion.

The next phase of development of the human vascular system is illustrated by the well-known embryo Glaevecke 1·54 mm. of Graf Spee ('89, '96). Here again, as in the preceding stage, vascular rudiments are seen on the yolk-sac and in the chorion, but, in addition to these, it is possible to note the first intra-embryonic vascular rudiments.

In embryos of 5 somites and upwards it is observed that the vitelline plexus has established its communications cranially with the heart by means of two channels, the vitelline veins, reaching as far as the first intersegmental cleft, as Dandy ('10) first showed, while caudally, in the region of the unsegmental mesoderm, the branches of the vitelline arteries form a plexus of capillary-like vessels from which, as shown by Felix ('10) and confirmed by Evans ('12), the umbilical artery takes its origin.

The Heart and Pericardium.

In mammals much has been done to throw light upon the development of the heart, notably by His ('81, '85, '86) and Bischoff ('42, '52), in rabbits, Born ('89), in dogs, Bonnet ('91, '01, '07), in pigs, Keibel ('88), and in ferrets, Yeates ('11), but many gaps must be filled up before it is possible to obtain a clear conception of the details of its formation.

Tandler ('12) says "the earliest developmental processes of the heart, especially in so far as they concern the formation of the endothelium of the heart and vessels, are unknown in the human embryos, but probably one will not be far astray in assuming that the earliest rudiment of the human heart is essentially similar to that of the mammalia." The earliest stages of development of the mammalian heart are undoubtedly intimately associated with the development of the blood-vessels, but concerning the latter various opposing views have been formulated and already been dwelt upon in the beginning of this communication.

It is clear that the precise mode of development of the blood-vessels is not yet definitely established, and a short survey of the early stages of the development of the heart will show that our knowledge of that subject also is deficient. In mammals, according to Mollier ('06), the first rudiment of the heart is the appearance of a number of cells, which are discernible in embryos of 2–3 primitive somites. The vascular cells appear between the entoderm and mesoderm on both sides not far from the median plane of the embryo, at first in the distal portion of the

head. They are responsible for the formation of the endothelium of the heart tubes only, the remaining constituents of the wall of the heart—that is, the myocardium and the epicardium—being derived from that part of the visceral cœlomic wall which has been designated by Mollier ('06) the heart-plate or cardiogenic plate.

It is generally held that the first aggregation of the vascular cells of the mammalian heart is paired and is situated ventral to the cœlomic cavity. By a process not yet satisfactorily explained, spaces soon make their appearance in the vascular cell mass, and when these spaces coalesce, two endothelial tubes are thus formed, one on either side of the median plane of the embryo. A fusion of the two endothelial tubes next takes place, and the unpaired heart tube is formed from the paired heart rudiments, but exactly how this fusion is brought about, opinions differ.

It was for long believed (Balfour ('81), Hensen ('76), Hertwig ('92), Kölliker ('61), and it is still held by some (Tandler ('12), Bryce ('08), Bailey ('12), Wilson ('14), H. von W. Schulte ('15), and others) that in mammals, as in birds, the two endothelial tubes, out of which the heart is formed, appear at a time when the lateral folds, which are said to form the ventral wall of the throat, are only just visible, that, as the lateral folds of the splanchnic walls increase, the two halves of the heart, enclosed within the hitherto symmetrical and laterally placed pleuro-pericardial cavities, become carried medially and ventrally until they fuse on the ventral side of the fore-gut, and that the heart is therefore provided, at least for a time, with a ventral and a dorsal mesocardium.

In the chick, a ventral mesocardium is recognisable, but this is due, as Robinson ('02) points out, to the relatively late penetration of the mesoderm in the cranial region. In amphibians lateral folds have been described, but it is erroneous to presume that such folds, which, by virtue of their fusion ventrally, form the ventral wall of the fore-gut, really occur in mammals. In the latter, the pericardial mesoderm appears in the pericardial portion of the embryonic area, and it is there completely differentiated into somatic and splanchnic layers before the head bend is developed; there is therefore a single pericardial cavity to begin with, which extends from side to side along the cranial boundary of the embryonic area. As the head bend develops, the single pericardial cavity is reversed, and it is carried into the ventral wall of the fore-gut, where it forms a U-shaped tube which communicates at each end with the general cœlom. The heart rudiments are formed in the splanchnic layer of the pericardial mesoderm; therefore, after the reversal of the area they lie in the dorsal wall of the pericardial cavity attached only

by a dorsal mesocardium to the ventral wall of the fore-gut, but they are never, at any time, connected with the ventral wall of the pericardium by a ventral mesocardium.

Rouvière ('04), on the other hand, while he agrees with Robinson as to the absence of the ventral mesocardium in mammals, gives a different account of the process which leads to the closure of the fore-gut. He describes the formation of the lateral pleuro-pericardial canals, which grow cranially round the cranial end of the brain-plate and fuse to form a continuous channel. The splanchnopleure forming the caudal wall of the pleuro-pericardial cavity now forms a continuous fold, which Rouvière calls the cardiac fold and which he describes as growing actively backwards as a whole. Gräper ('12), in a description of the growing processes in the developing chick, asserts that there is considerable evidence in support of the view that the margin of the fore-gut (umbilical orifice) moves caudally concurrently with the growth of the head fold cranially.

Miss Parker ('15), in her studies of the early stages in the development of Marsupials, summarises her statement by saying "that while the initiation of head-fold formation is in all probability due to the forward growth of the brain-plate, there occurs also an active backward growth of the anterior intestinal portal (umbilical orifice)."

Shore ('89) describes that the head fold of the chick embryo results from a growth of the head forwards over the diblastic part of the blastoderm, and that a "folding off" does not occur, at any rate at first.

Recently Watt ('15), in his investigation into two young twin human embryos with 17–19 paired somites, states: "From the atrial canal the ventricle continues on at the left and runs far forward in the pericardial cavity, when it is strongly flexed ventrally and turns caudad as it reaches the median line. It is here attached to the pericardial wall by a short stretch of ventral mesocardium, the only portion of this structure which is still present." Though a small piece of dorsal mesocardium is depicted in his paper (plate 3, fig. 4, and plate 4, fig. 2), there is nothing to indicate the existence of the ventral mesocardium which Watt describes.

Stage I.

The material for this stage consists of three embryos. Selected sections of each of these specimens have been photographed to show the conditions and relationships of the blood-cells and vascular endothelium.

(*a*) Ferret Embryo, 1·15 mm. (F.C.Q.Z.(Z)).

General Description.

The germinal area of this embryo measures 1·4 mm. No mesodermic somites can be detected, and there is no indication of a heart rudiment. The head fold has not yet begun to develop, and no intra-embryonic blood-vessels can be found in the specimen.

There is, however, a shallow neural groove which terminates at the primitive caudal and subsequently dorsal end of the bucco-pharyngeal membrane. The groove broadens out caudally. Beneath the caudal end of the neural plate it becomes the chordal canal. The chordal canal

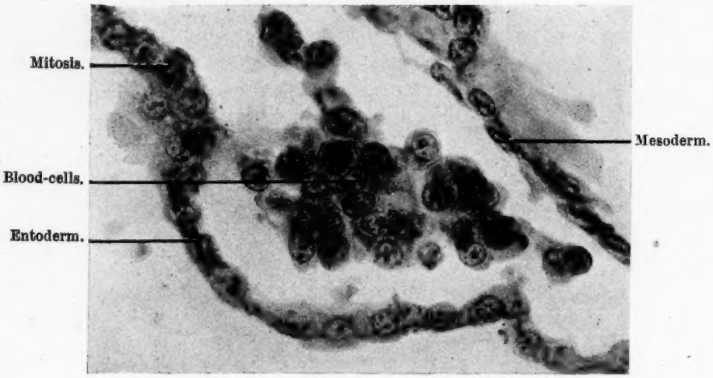

FIG. 1.—Showing blood-cells. ×500.

terminates caudally in a mass of cells which fuse with the ectoderm at the cranial end of the primitive streak.

Blood-Cells.

Though no intra-embryonic blood-vessels can yet be found in this specimen, extra-embryonically there are solid clusters of blood-cells which are not surrounded by any endothelium (fig. 1). In none of the clusters of blood-cells is it possible to detect that the peripheral layer of the cells resolves into endothelium. The cells forming the clusters are spheroidal in shape, lying between the mesoderm and the entoderm. They are provided with large well-stained nuclei, and are very often adherent to the entodermal cells, which exhibit characters similar to those of the blood-cells. No lumen can be found in any of the blood clusters.

The mesodermal cells spread out in a thin layer to cover the adjacent

yolk-sac. They are spindle-shaped, and are attached to each other by long protoplasmic processes.

Fig. 1 shows a portion of the extra-embryonic area in which a cluster of blood-cells is seen lying free between the mesoderm and the entoderm. The cells forming the mesoderm are, as noted, spindle-shaped, whilst the cells constituting the entoderm are spheroidal and exhibit other characters which are similar to those of the blood-cells. Mitotic division occurring in one of the entodermal cells can be detected in the neighbourhood of the blood clusters (fig. 1). It is proved that this is not a singular occurrence by the fact that a similar phenomenon is again seen in the entoderm of another embryo (Stage II. (*b*), figs. 15*b*, 17*a* and *b*).

(*b*) Ferret Embryo, 1·6 mm. (F. 1904, QZ., U2).

General Description.

This embryo measures 1·6 mm. after it has been cut. There is, as yet, no mesodermic somites. The heart rudiment is absent, and no intra-embryonic blood-vessels can be detected. There is, of course, no head fold. A primitive streak is, however, present, and there is a primitive groove.

The notochord is tubular at its caudal end. In parts its ventral wall opens into the yolk-sac. Its caudal extremity is fused with the ectoderm at the cranial end of the primitive streak, as in the previous specimen. Cranial to the primitive streak a faint neural groove is present on the surface of the embryo. It terminates, as in the previous case, at the buccopharyngeal membrane cranially.

Blood-Cells.

In this specimen blood-cells are found abundantly on the wall of the yolk-sac between the mesoderm and the entoderm. The blood-cells are spheroidal in shape, provided with large well-stained nuclei, as in the preceding specimen. They are arranged in solid clusters, without any lumina in them, and are devoid of any endothelial coverings (figs. 2*a*, 2*b*, and 3). The majority of the cell clusters are found to be adherent to the entodermal cells, which exhibit characters similar to those of the blood-cells (fig. 2*b*).

The mesodermal cells, covering the adjacent yolk-sac and in the neighbourhood of the blood-cells, are arranged in a thin layer which is not in contact with the entoderm. They are spindle-shaped, and are connected with one another by long protoplasmic processes, as previously noted (fig. 2*a*).

FIG. 2*a*.—Showing blood-cells. ×500.

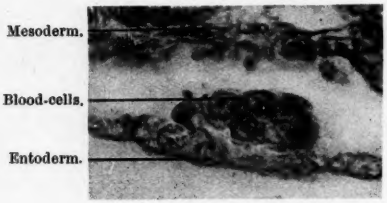

FIG. 2*b*.—Showing blood-cells. ×500.

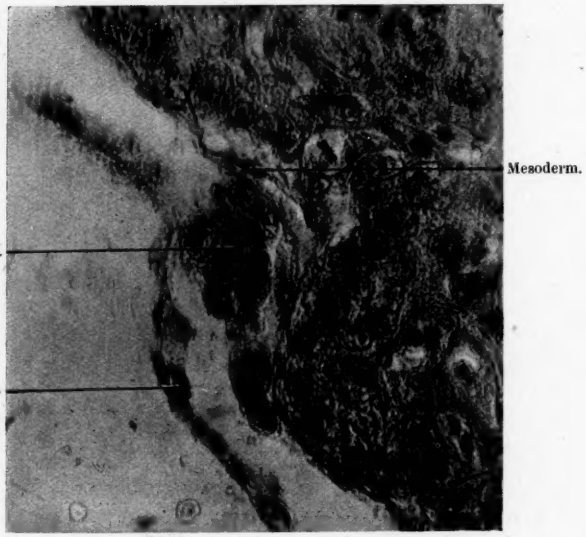

FIG. 3.—Showing blood-cells. ×500.

(*c*) Ferret Embryo, 1·74 mm. (F. 1904, Q.A.A. U1) with 3 Somites.

General Description.

The primitive streak is well marked, and is notched at the caudal part of its extent by the primitive groove. The mesoderm, covering the caudal part of the embryonic area, is thickened, and indicates the position of the allantoic mesoderm. Cranially the mesoderm of the primitive streak fuses with the caudal end of the chorda.

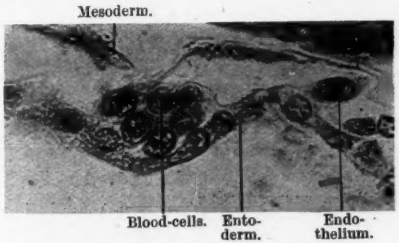

FIG. 4.—Showing blood-cells. ×500.

There is a broad, shallow neural groove which narrows cranially, and its walls become much thickened in the position which is occupied by the trigeminal ganglion. The groove gradually disappears, and becomes continuous cranially with the bucco-pharyngeal membrane.

There is no heart rudiment. The two pleuro-pericardial canals are present one on each side of the embryo, but these have not grown across the median plane cranially; consequently there is no pleuro-pericardial cavity. No intra-embryonic blood-vessels can be detected.

Blood-Cells and Endothelium.

Extra-embryonically clusters of blood-cells are found scattered over the greater part of the yolk-sac, to which they are often adherent (fig. 4). The

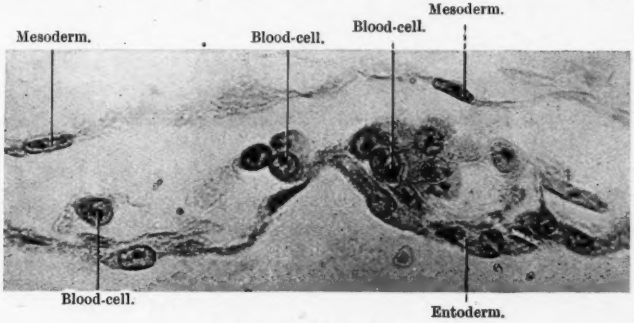

FIG. 5.—Showing blood-cells. ×500.

characters of the blood-cells, the entoderm and the mesoderm are similar to those already seen in Stage I., (*a*) and (*b*) specimens. The mesodermal cells (fig. 5) are, however, more flattened, and are connected with each other with longer protoplasmic processes than those observed in the previous specimens. In addition to the blood-cells, endothelial cells can be detected here and there in the extra-embryonic region lying between the mesoderm and entoderm. These endothelial cells, unlike the blood-cells, are spindle-shaped (fig. 4), and can be traced in some cases to their mesodermal origin.

Stage II.

The material for this stage consists of two embryos, one measuring 1·97 mm. in length with 5 somites, and the other 2·3 mm. with 6 somites.

(*a*) Description of the Graphic Reconstruction of the Heart and Cranial Portion of a Ferret Embryo 1·97 mm. in Length with 5 Somites. (F.B.A.A., G.A.)

This is the youngest specimen of the series of ferret embryos selected for the purpose of reconstruction in this investigation. Its total length measures 1·97 mm. after preparation and embedding. It may be mentioned that the sections, each of which is 10 μ in thickness, are perfect, and that the histological condition is excellent.

General Description.

No plastic reconstruction of the embryo was made, for it appeared that a graphic reconstruction of the heart would be sufficient for the purpose in hand.

The neural groove and the primitive streak are both present. The neural tube is deepest at the brain region, where it shows thickenings which correspond to the positions of the trigeminal and otic ganglia. The cranial end of the neural groove gradually shallows until it disappears at the primitive caudal end of the bucco-pharyngeal membrane.

Vascular System.

In this specimen the heart is represented merely by a transverse blood channel which lies across the median plane and unites the cranial ends of the two vitelline veins (figs. 6*a* and *b*). It is bounded caudally by the bucco-pharyngeal membrane, and cranially by the pleuro-pericardial cavity (fig. 6*a*). The cranio-caudal diameter of the heart rudiment is 20μ, its breadth, 120μ. The rudiment of the pleuro-pericardial cavity is present. It is that portion of the cœlomic space which crosses the median plane of

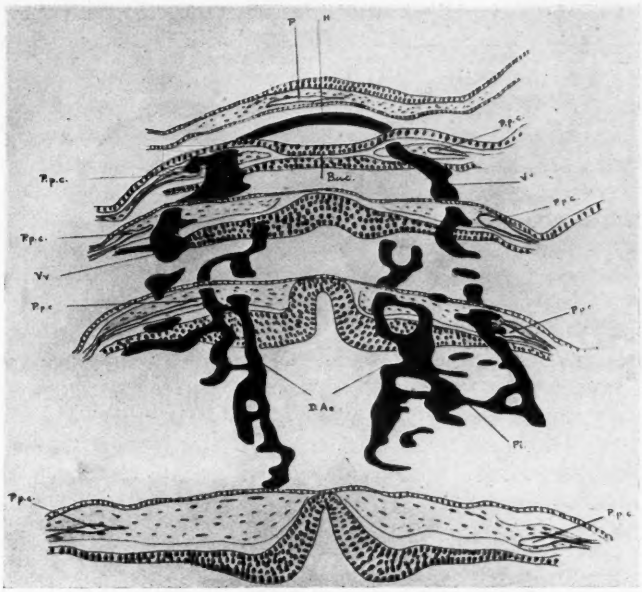

FIG. 6*a*.—Graphic reconstruction. ×200.

P., pericardium; H., heart rudiment (primary union); P.p.c., pleuro-pericardial canal; V.v., vitelline vein; D.Ao., dorsal aortæ; Pl., plexus; Buc., bucco-pharyngeal membrane.

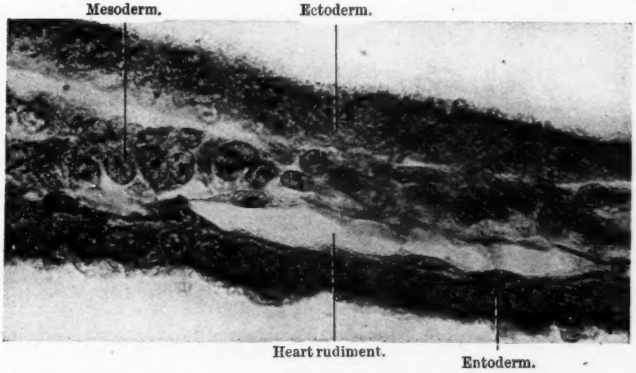

FIG. 6*b*.—Transverse section through primary heart tube. ×500.

the embryonic area cranial to the rudiment of the heart and is closed cranially and caudally, and on each side it is connected with the pleuro-pericardial canal (figs. 6*a* and 7). Together with the pleuro-pericardial

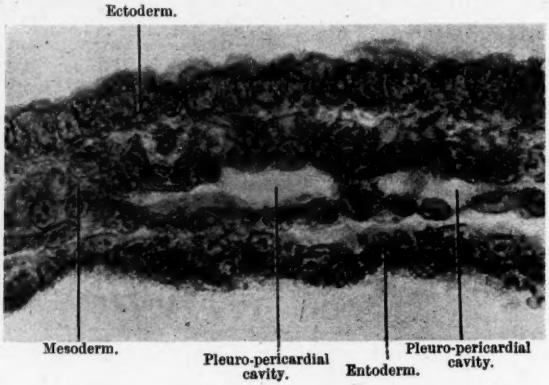

FIG. 7.—Transverse section through pericardium. × 500.

canals it forms an inverted U-shaped canal (fig. 6*a*), which lies dorso-cranial to the vitelline veins and the heart rudiment (fig. 8).

Each vitelline vein is placed ventral to the corresponding pleuro-

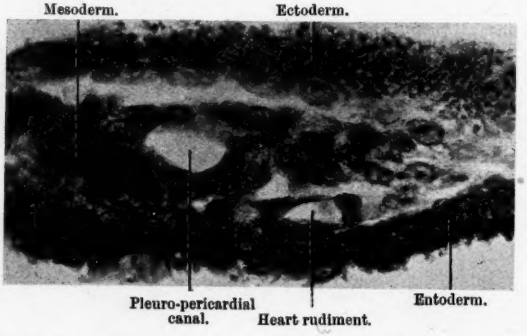

FIG. 8.—Transverse section through pericardium and heart. × 500.

pericardial canal and lateral to the dorsal aorta of the same side (figs. 6*a* and 9). The two veins converge cranially, and each terminates in the corresponding end of the heart rudiment cranial to the bucco-pharyngeal membrane (fig. 6*a*).

There are two rudiments of the dorsal aortæ (fig. 6*a*). They run caudo-

cranially one on each side of the medullary groove. They are still more or less plexiform in character, and they terminate blindly at their cranial extremities some distance caudal to the heart rudiment.

Communications between the dorsal aortæ and the corresponding vitelline veins are described by Bremer ('12) in a 3·4 mm. rabbit embryo. Such communications (fig. 6*a*) can be traced in the caudal portion of the ferret embryo at this stage, which, so far as its general development is concerned, is considerably younger than Bremer's embryo. Caudally the dorsal aorta breaks up into a plexus spreading over the wall of the yolk-sac.

There is, of course, no ventral mesocardium, and the head fold and foregut are not yet developed. As far as the pericardial cavity and the pleuro-pericardial canals are concerned, this specimen does not differ, to any great

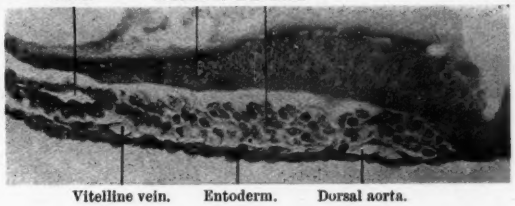

FIG. 9.—Transverse section through embryo. ×200.

extent from what has been described in *Dasyurus viverrinus* (7·5 mm. vesicle) by Miss Parker ('15). The heart of the ferret embryo is, however, in a more advanced stage of development than the 7·5 mm. Dasyurus, in which the heart rudiment is represented merely by some scattered angioblast cells and strands of cells, and in which the vitelline veins terminate cranially at the level of the caudal limit of the trigeminal rudiment. In the ferret specimen under consideration the walls of the vessels of the vitelline plexus are in direct continuity with the adjacent splanchnic mesoderm (figs. 10*a*, *b*, and *c*), a fact which is of interest in association with the mesoderm origin of the walls of the vessels.

(*b*) Description of a Ferret Embryo 2·3 mm. with 6 Pairs of Somites. (F. 1904, B.G.a.)

General Description.

The primitive streak is present. Its cranial extremity is continuous with the notochord, which shows indications of the notochordal canal, and the notochord has begun to dovetail with the entoderm. More cranially

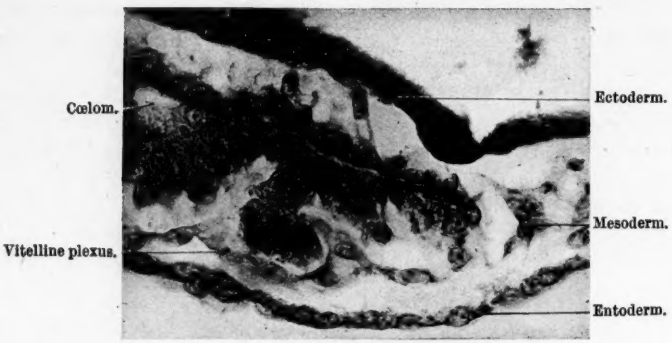

FIG. 10*a*.—Transverse section through embryo, showing endothelium. ×375.

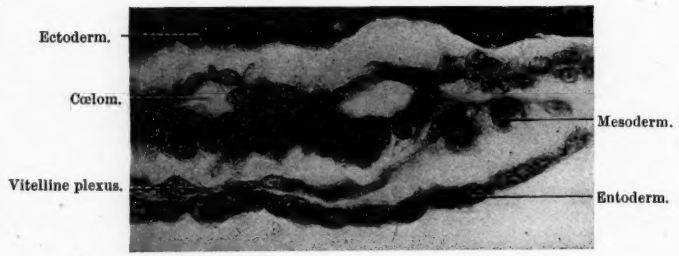

FIG. 10*b*.—Transverse section through embryo, showing endothelium. ×375.

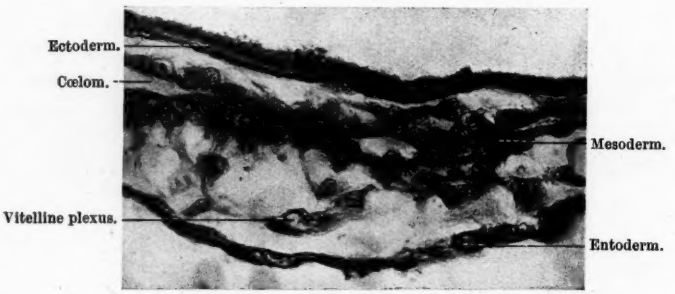

FIG. 10*c*.—Transverse section through embryo, showing endothelium. ×375.

the notochord is entirely fused with the entoderm, and for some ten sections cranial to the primitive streak it can scarcely be distinguished except by the height of the cells from the entodermal cells.

The neural groove extends caudally to the primitive streak. It is wide and shallow at the caudal end, but deepens and narrows as it passes cranialward between the laterally placed mesodermal somites, and cranial to the somatic region the walls of the neural groove show thickenings which correspond in positions to the auditory and trigeminal areas. The neural groove then gradually shallows until it disappears at the caudal end of the bucco-pharyngeal membrane.

Vascular System.

This embryo exhibits several features which were not present in the preceding specimens. No reconstruction was made at the time, but a

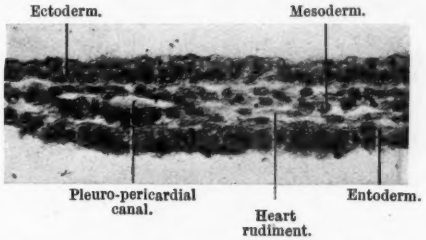

FIG. 11*a*.—Transverse section through pericardium and heart. × 200.

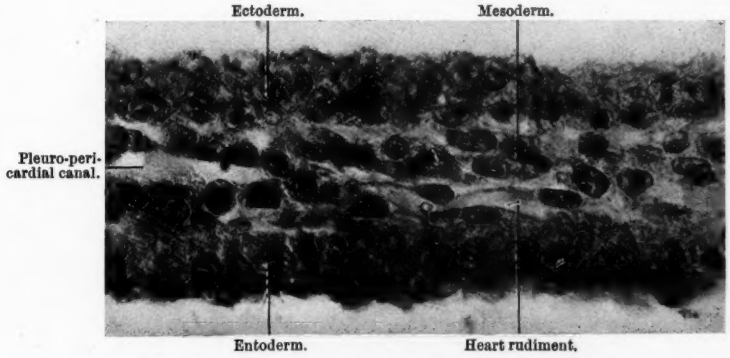

FIG. 11*b*.—Transverse section through pericardium and heart. × 500.

study of the sections shows that the embryo as regards general development is slightly in advance of the previous specimen. The heart and pericardium

(fig. 11*a*), have practically not changed, the former lying ventral to the latter. Figs. 11*a* and *b* illustrate the union of the two heart tubes

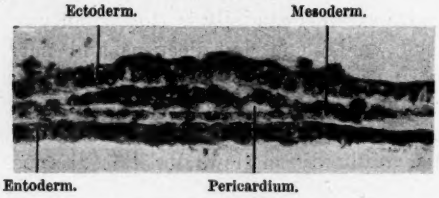

FIG. 12*a*.—Transverse section through pericardium. × 200.

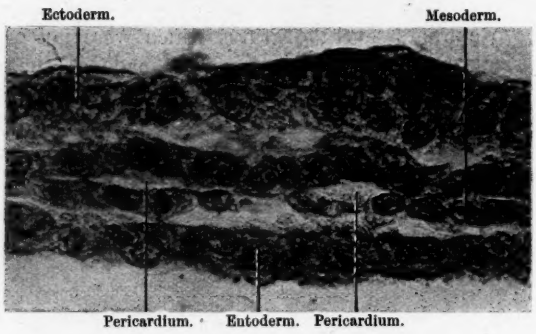

FIG. 12*b*.—Transverse section through pericardium. × 500.

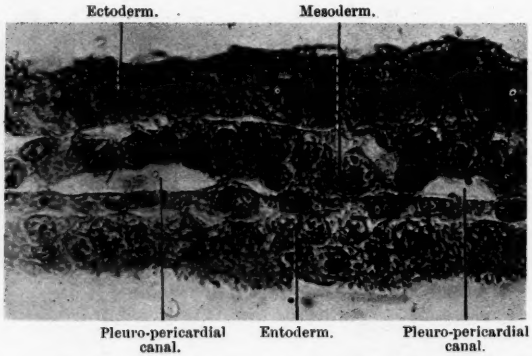

FIG. 12*c*.—Transverse section through pleuro-pericardial cavity. × 500.

across the median plane, and immediately cranial to this the pericardium is seen stretching transversely to communicate on either side with the

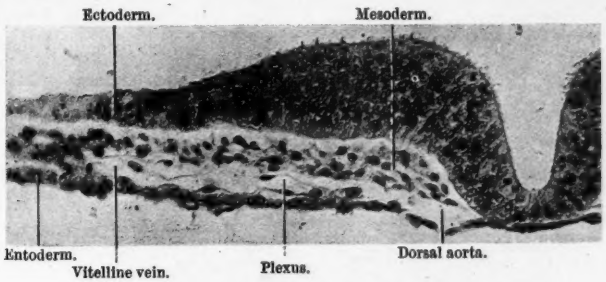

FIG. 13.—Transverse section through embryo. ×200.

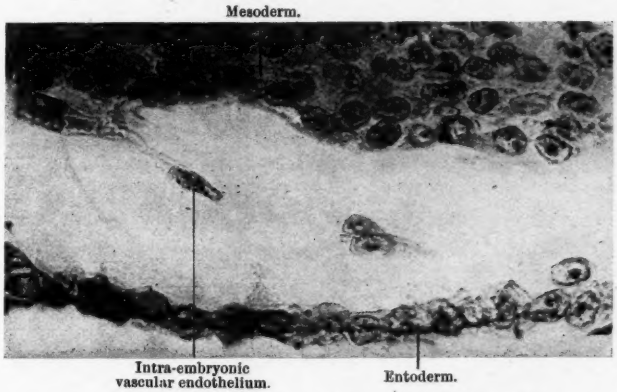

FIG. 14*a*.—Transverse section showing endothelium. ×500.

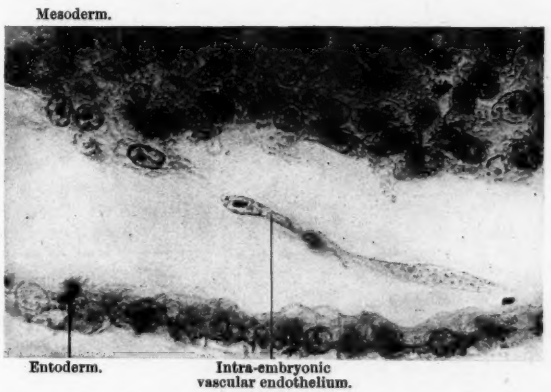

FIG. 14*b*.—Transverse section showing endothelium. ×500.

pleuro-pericardial canal (figs. 12*a*, *b*, and *c*). In the 1·97 mm. ferret embryo (Stage II. (*a*)), it has been noted that there is a communication between the

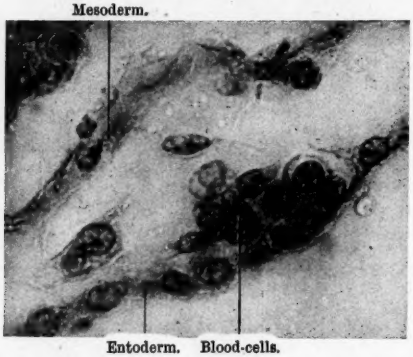

FIG. 15*a*.—Showing blood-cells. × 500.

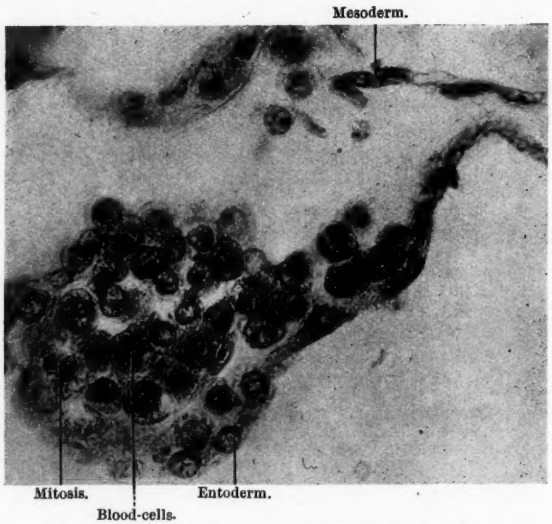

FIG. 15*b*.—Showing mitosis in entodermal cells to form blood-cells. × 500.

vitelline vein and the dorsal aorta. Such a communication is seen also in this specimen (fig. 13). Some of the intra-embryonic vascular endothelium can be traced to its origin from the mesoderm (figs. 14*a* and *b*).

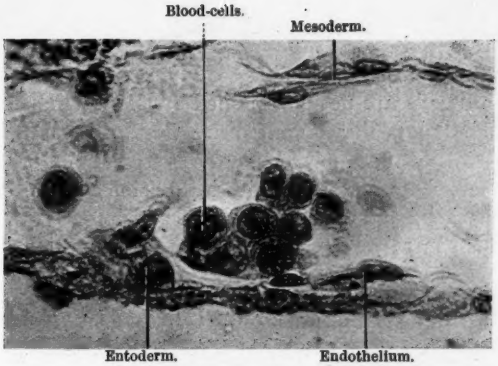

FIG. 16.—Showing endothelium and blood-cells. × 500.

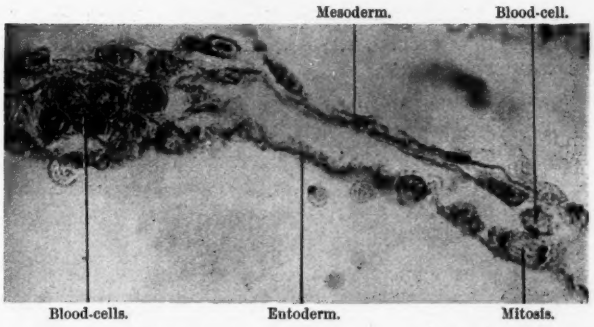

FIG. 17*a*.—Showing mitosis in entoderm to form blood-cells. × 500.

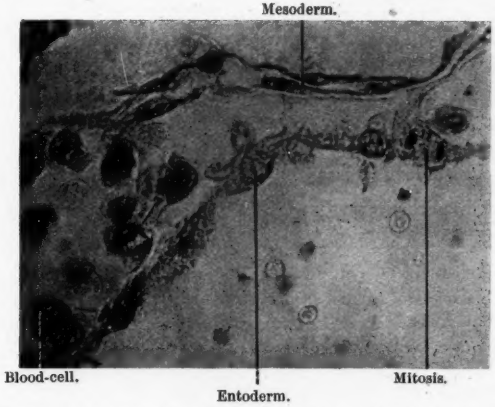

FIG. 17*b*.—Showing mitosis in entoderm to form blood-cells. × 500.

In this specimen it is possible to detect that some of the intra-embryonic blood-cells are not surrounded by endothelium (figs. 15*a* and *b*), whilst others are partially engulfed by flattened vascular endothelium (fig. 16). Figs. 15*b*, 17*a* and *b*, taken from sections of the caudal end of this specimen, show distinctly mitotic divisions in the entodermal cells in the neighbourhood of some blood-cells.

There is no ventral mesocardium, and the fore-gut has not yet begun to develop.

Stage III.

The material for this stage consists of one embryo which is 2·3 mm. in length and with 9 somites.

Description of the Graphic Reconstruction of the Heart and the Cranial Portion of a Ferret Embryo 2·3 mm. in Length with 9 Somites. (F. Ap. 16/28/08.)

General Description.

The amnion is closed caudally. The allantoic diverticulum and the allantoic mesoderm are both present. The neural groove extends to the caudal end of the embryo, but terminates, however, at some distance cranial to the tail amnion-fold. It narrows and deepens as it passes cranially.

The rudiment of the otic ganglion is distinct, and the rudiment of the trigeminal ganglion is likewise recognisable. The head fold has begun to form, and a portion of the fore-gut is also defined. There is no indication of the primary optic vesicle.

Vascular System.

The heart of this embryo has not yet been reconstructed in wax, but the graphic reconstruction (fig. 18) which has been made shows that, in length, this specimen is identical with the Stage II. (*b*) embryo, but in its general development it is decidedly in a more advanced stage than the preceding one, as the central part of the transverse rudiment of the heart seen in Stage II. (fig. 6*a*) has, in this specimen, begun to break up, for two non-vascular loculi have divided it incompletely into a cranial and a caudal portion (figs. 18, 19*a–e*). Apparently the division of the central part of the rudimentary transverse heart proceeds still further as development goes on, until it is completely separated into right and left halves, for in Stage IV. (fig. 27) the heart rudiment is represented by two separate longitudinal endothelial tubes which lie side by side and are in contact in their middle third.

Cranially two vessels, one on each side of the median plane, run cranial-

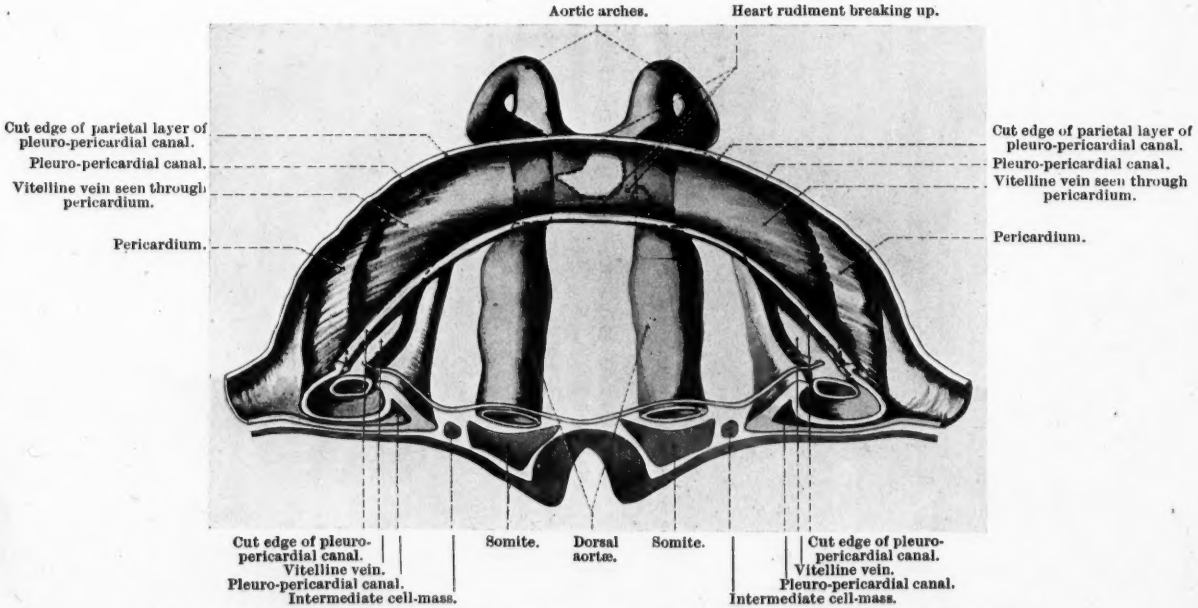

FIG. 18.—Showing primary heart tube breaking up to form two lateral heart tubes. × 100. (Semi-schematic.)

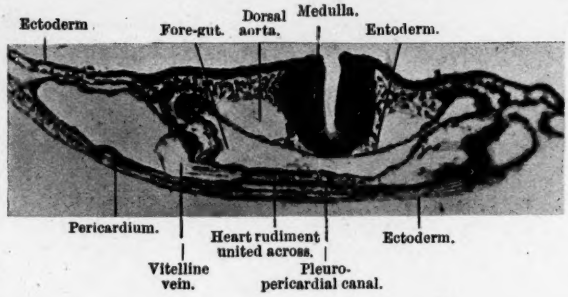

FIG. 19*a*.— × 100.

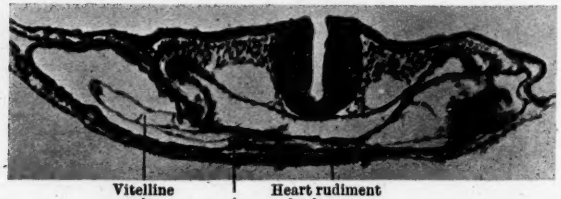

FIG. 19*b*.— × 100.

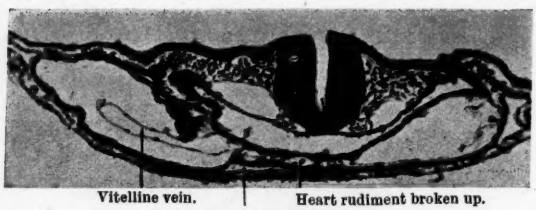

FIG. 19*c*.— × 100.

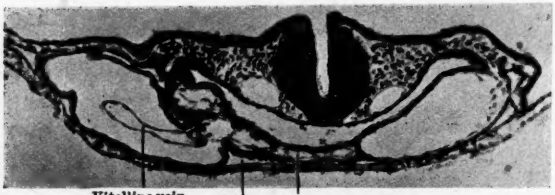

FIG. 19*d*.— × 100.

ward from the heart rudiment. They arch round the cranial end of the fore-gut and form the first cephalo-aortic arches, which terminate dorsally in the corresponding dorsal aortæ (figs. 18 and 20). Caudally the heart rudiment receives the two vitelline veins. It is obvious that the fore-gut has begun to develop *pari passu* with the head fold.

The pericardial cavity is much wider and longer than it is in the preceding specimen, measuring 870μ in the transverse diameter and 140μ in the antero-posterior direction. The two dorsal aortæ are well developed and run parallel to each other, one on each side of the median plane of the embryo, not far from the medullary groove (figs. 18, 19*a–e*). Here again there is nothing to indicate the presence of a ventral mesocardium.

This stage of development, as far as the heart is concerned, appears to fall in between the Stage II. *Dasyurus viverrinus* (8·5 mm.) and the

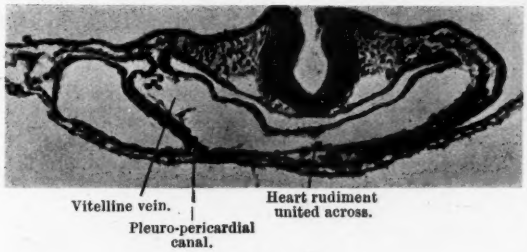

FIG. 19*e*.—×100.

Stage III. *Perameles nasuta* (7·5 mm., 11 somites) of Miss Parker ('15). In the Dasyurus the endothelial tubes have come actually in contact with each other at their extreme cranial ends, and presumably have united across the median plane of the embryo. It should be noted that the significance of this connection between the two vitelline veins across the median plane was not dwelt upon, and was considered only as being remarkable by Miss Parker, who states also "that lateral and caudal to the median union, each endothelial tube gives rise to the first aortic arch, which follows the antero-lateral margin of the gut almost to the median plane, and there becomes continuous with the corresponding dorsal aorta, the two aortæ being well developed at this stage."

It is quite possible that what has been taken for the first aortic arch in Miss Parker's Dasyurus specimen, as in the case of Eternod's human embryo ('95, '99), may, after all, prove to be the plexus which lies between the dorsal aorta and the vitelline vein, and which has been described by Bremer ('12) to be present in the rabbit embryo of 5 somites. If this is

the case, the Stage II. Dasyurus may be regarded as being similar with the Stage II. (*a*) ferret embryo, in so far as the development of the heart, the vitelline veins, and the dorsal aortæ is concerned.

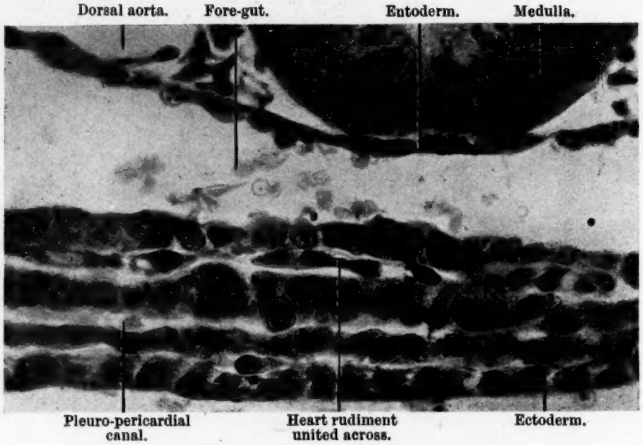

FIG. 19*a'*.—Showing primary heart tube. × 500. (Enlarged from fig. 19*a*.)

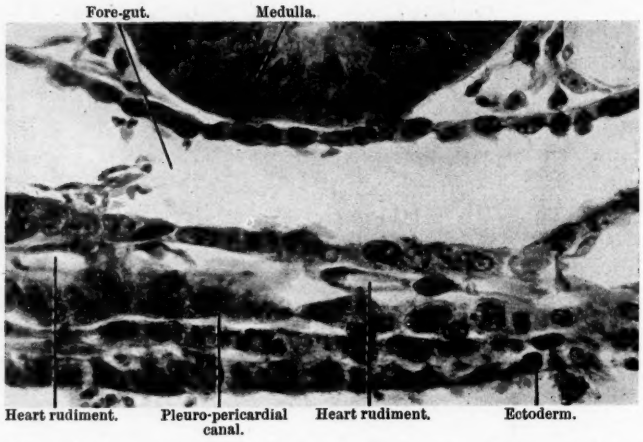

FIG. 19*b'*.—Showing primary heart tube breaking up. × 500. (Enlarged from fig. 19*b*.)

In the Perameles (7·5 mm.), the two heart tubes lie separate from each other ventral to the closed fore-gut. At the level of the umbilical orifice they diverge and lie on each side of the open gut in the dorso-medial wall

of the pericardium. From the cranial extremity of each endothelial tube there arise two vessels, one of which runs cranially and laterally towards

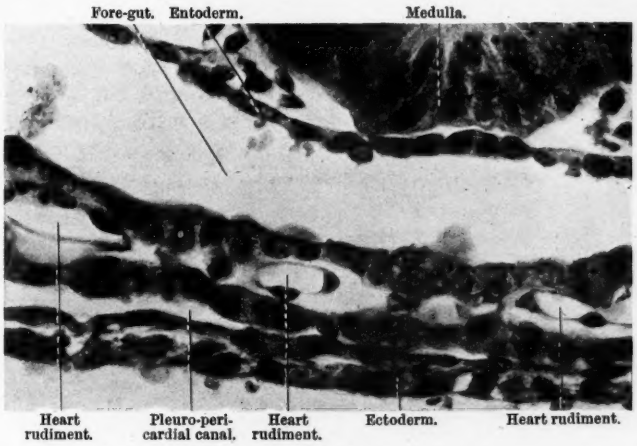

FIG. 19*c'*.—Showing primary heart tube breaking up. × 500. (Enlarged from fig. 19*c*.)

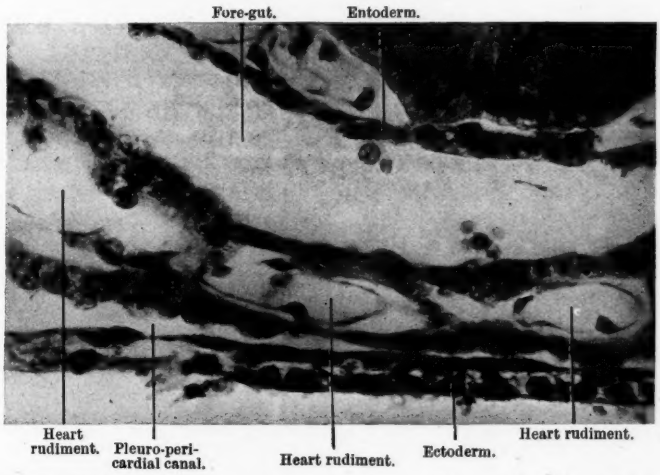

FIG. 19*d'*.—Showing primary heart tube breaking up. × 500. (Enlarged from fig. 19*d*.)

the lateral margin of the gut and then parallel with this margin. It loops round the cranial end of the gut, joins the dorsal aorta, and thus consti-

tutes the first aortic arch. The other vessel is small, and runs caudally and laterally, lateral to and almost parallel with the heart tube. This,

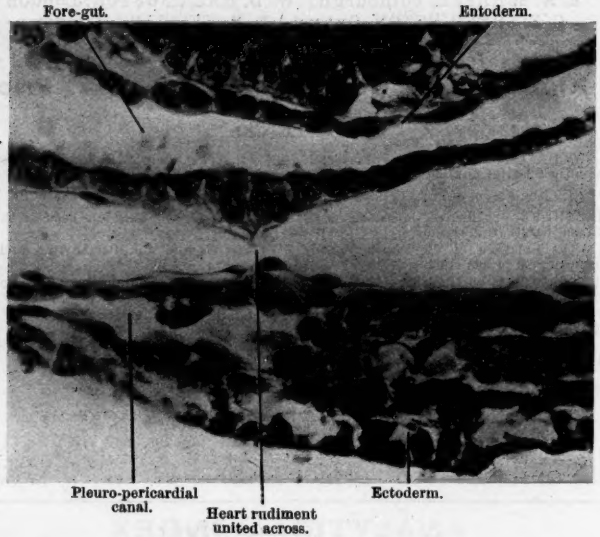

FIG. 19*c'*.—Showing primary heart tube. × 500. (Enlarged from fig. 19*c*.)

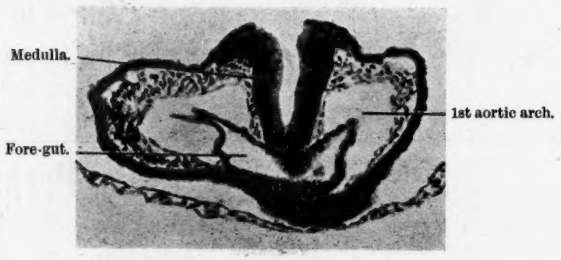

FIG. 20.—Showing first aortic arch. × 100.

according to Miss Parker, is the ventral portion of the future second aortic arch. In the median space between the cranial ends of the endothelial heart tubes are a number of scattered angioblast cells lying between the splanchnic mesoderm and the entoderm.

(*To be completed in January Part.*)